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Symposium

Phenological Shifts in Plants and Pollinators over a Century Disrupt Interaction Persistence*

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abstract: Mutualistic interactions between plants and pollinators play an important role in supporting biodiversity and ecosystem stability. However, these interactions are increasingly threatened by climate change, which can alter the phenology of species and cause temporal mismatches between interacting partners. Leveraging historical and contemporary datasets collected more than a century apart, we investigated phenological shifts in plants and pollinators and the impact of changes in temporal overlap of the interaction partners on the persistence of their interactions. We found that the onset of flowering and insect activity generally started earlier and has lasted longer in the present. We also found that greater temporal overlap of plant and pollinator species predicted a higher probability of persistence of their interaction between time periods. Our results document phenological shifts over a century and emphasize the importance of maintaining phenological matching for the persistence of plant-pollinator interactions. This illustrates the value of historical datasets for understanding long-term ecological dynamics in the face of accelerating environmental change.

Keywords: pollination ecology, climate change, interaction networks, long term, historic data.

Introduction

Mutualistic interactions between plant and pollinator species play an important role in supporting ecosystem diversity and stability (Hale et al. 2020). These interactions facilitate critical ecosystem services, such as pollination, which is essential for the reproduction of most wild and cultivated plants (Klein et al. 2007; Ollerton et al. 2011). The long-term stability of these mutualistic interactions therefore ensures the continued availability of resources for a wide range of organisms, thereby supporting biodiversity and ecosystem health. However, plant-pollinator interactions currently face a range of threats, including land use change, agrochemicals, and climate change. Climate change is emerging as a growing threat to biodiversity (Halsch et al. 2021). One of the most conspicuous ecological impacts of global warming concerns changes in phenology—the seasonal timing of life history events (Ovaskainen et al. 2013). Changes in phenology may alter the timing of interactions between plants and pollinators, potentially disrupting their mutual relationships (Forrest 2015).

Organisms respond to climate warming in various ways. Plants often respond to warming by advancing the timing of flowering (Menzel et al. 2006; CaraDonna et al. 2014). However, these changes are not distributed equally across the growing season, as some early-flowering species tend to change their phenology more than later-flowering species (Miller-Rushing and Inouye 2009; Kopp et al. 2020; Inouye 2022). For example, an earlier snowmelt can allow for an earlier start of plant growth and potentially for a longer growing season (Livensperger et al. 2016; Inouye 2022; Dunne et al. 2003). Terrestrial insects similarly show a general trend toward phenological advancement, but populations can differ in response to climate change (Duchenne et al. 2020).

Phenology of individual species plays a critical role in shaping species interactions. Plants and pollinators must overlap in space and time to interact, and changes in phenology can disrupt these interactions (Hegland et al. 2009; Vázquez et al. 2009; Olesen et al. 2010; Nakazawa and Doi 2012). Shifts in species' phenology can lead to decreasing

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temporal overlaps in species occurrence (Memmott et al. 2007; CaraDonna et al. 2014). For example, warmer temperatures can lead to pollinators emerging before or after their primary food sources are available (Visser and Both 2005; Kharouba et al. 2018). Mismatches between plant flowering times and pollinator activity can disrupt mutualistic interactions with potentially detrimental effects, such as reduced pollination services and altered plant reproductive success, community structure, and ecosystem resilience.

Matching the tempo of their climate drivers, phenological shifts happen slowly, usually taking decades for trends to become apparent. Thus, understanding phenological changes and their consequences requires long-term studies. However, long-term data on plant-pollinator interactions are rare, as most datasets span 1–4 years (Schwarz et al. 2020; CaraDonna et al. 2021). This scarcity of long-term data presents a significant challenge in understanding and predicting the impacts of climate change on ecological interaction networks, which represent the relationships between species, such as pollinators and plants. Historic data on species interactions can provide a valuable look into the state of species interactions and ecosystems in the past, and resampling historical study systems can provide valuable insights into how they have changed across long time spans (Rakosy et al. 2022). For example, studies using historical data to compare plant-pollinator interactions over more than a century have found notable changes in community composition of pollinators and significant shifts in plant-pollinator interactions (Burkle et al. 2013; Zoller et al. 2023). These results highlight the importance of long-term data in understanding the impacts of climate change on communities and species interactions.

Here, we compared historical and present data collected over a century apart in a region where temperature has increased but potentially confounding factors, such as land use, have changed minimally. We assessed phenological shifts in plants and pollinators and investigated potential temporal mismatches between plants and pollinators. Specifically, we asked two main questions. First, how does the phenology (onset, central tendency, end, and duration) of plant flowering and pollinator flight activity change across time periods? And second, does change in temporal overlap of interacting species predict persistence or loss of interactions? For the first question, we hypothesized that plants and pollinators respond to climate warming by advancing their phenologies. Warmer temperatures are known to trigger earlier flowering and emergence in many species (Menzel et al. 2006; Hegland et al. 2009; CaraDonna et al. 2014; Duchenne et al. 2020); hence, we predicted that the onset of flight and flowering occurs earlier in the present compared with the past. Less is known about the timing of flight and flowering end dates, as they are influenced by a variety of factors, such as temperature, resource availability, and species-specific life history traits. However, if warming has extended favorable conditions later into the season over time, we would expect longer flight and flowering durations in the present (Dunne et al. 2003).

For the second question, we hypothesized that phenological shifts are asynchronous between plants and pollinators, reducing their temporal overlap and leading to a decrease in interaction persistence. These mismatches may arise because different taxa respond to environmental cues at different rates, with plants and pollinators potentially responding to distinct phenological drivers, such as temperature and photoperiod (Villagomez et al. 2021). Alternatively, even if both groups respond to the same drivers, differing magnitudes of response can still lead to misalignments (Kudo 2014; Weaver and Mallinger 2022). Thus, we predicted less temporal overlap between interacting partners in the present compared with the past, with species pairs experiencing lower temporal overlap being less likely to have persisting interactions.

Methods

Data Collection

Study Site. Data for the historical dataset that was resampled originated from Clements and Long (1923) and were collected on the slopes of Pikes Peak, Colorado (fig. S1; figs. S1–S6 are available online). With an elevation of 4,302 m, Pikes Peak is the highest summit of the southern Front Range of the Rocky Mountains. Pikes Peak lies in the Pikes National Forest, parts of which belong to the National Wilderness Preservation System, meaning that they are designated for preservation in their natural condition. Therefore, land use in the area has changed little over the last decades. However, Colorado, likely including the region around Pikes Peak, has experienced notable climatic changes during the last century. Temperatures in Colorado have significantly warmed since the beginning of recording in the late-nineteenth century with a statewide average temperature change of +1.61°C (2.9°F) between 1895 and 2022. Winter warming is the most pronounced, with an average change of +1.83°C (3.3°F) between 1859 and 2022 (Bolinger et al. 2024). No significant change in precipitation patterns during this period was detected (Bolinger et al. 2024). However, it has been shown that snowpack—which melts in spring and summer and provides water to plants, animals, and people—has drastically declined in the western United States, including the Pikes Peak region, in the past decades (Mote et al. 2018; Musselman et al. 2021).

Past Plant and Pollinator Data. Starting in 1910, Frederic E. Clements and Frances L. Long collected an extensive dataset on plants and their pollinators (Clements and Long

1923). Data collection took place mostly in the vicinity of the Carnegie Institution's Alpine Laboratory, a botanical research facility directed by Clements situated 2,600 m asl on the eastern slope of Pikes Peak (Clements and Long 1923; Resasco et al. 2024). Data collected by Clements and Long included information on the observed plant species, the pollinator species visiting the plant, the date of observation, and the frequency of visits. Data were collected over multiple years; however, while most records had a day and month reported, the collection year was not available for most observations. The data were published by Clements and Long (1923), which we digitized and cleaned, updating species names to current taxonomy (using Snow [2009] and the GBIF Backbone Taxonomy [GBIF Secretariat 2023]) to allow for meaningful comparisons with present data.

Present Plant and Pollinator Data. During the years 2019–2022, new data on plant-pollinator interactions were collected by resampling Clements and Long's (1923) sampling area on the slopes of Pikes Peak. Observations of flowers and pollinators were conducted by surveying open flowers along hiking trails, meadows, roadsides, and other accessible locations across the study area. Sampling was conducted in diverse habitats to capture the variety of flowering plants. We sampled from late May to late August/early September, a period that largely overlapped with the historical dataset (fig. S2). During the early sampling period, flower observations were conducted at lower elevations, as flowers at the focal elevations (see below) had not yet started blooming. As the season progressed and flowers began to bloom at higher elevations, we moved our sampling efforts upward. We collected information on plant species and their pollinators, date of observation, and frequency of visits. We documented interactions by observing flowers along an elevation gradient on Pikes Peak, with particular focus on sites at similar elevations as the Alpine Laboratory. Sampling occurred in ecologically diverse areas characterized by high floral abundance and diversity, in an effort to ensure the representation of a broad range of species. We observed pollinators directly on flowers during sampling. We paid specific attention to flowering plant species emphasized by Clements and Long (1923), including *Aconitum columbianum*, *Chamerion angustifolium*, *Delphinium ramosum*, *Frasera speciosa*, *Geranium caespitosum*, *Mertensia lanceolata*, *Monarda fistulosa*, *Penstemon glaber*, *Penstemon secundiflorus*, *Penstemon virens*, *Rosa acicularis*, *Rubus deliciosus*, and *Rubus idaeus*, which were observed for extended periods.

Data Selection

Unless stated otherwise, we included only species in the analyses that met the following criteria: (1) species were observed in both the past and the present and were identified to species level; (2) species were observed for at least 3 days in each time period; and (3) at least three individuals of the species were observed in each time period. In total, 25 pollinator and 11 plant species fulfilled these criteria (table S2; tables S1–S5 are available online). The pollinator species included one species belonging to the order Diptera (*Eristalis stipator*) and one species belonging to the order Lepidoptera (*Poanes taxiles*), while the other 23 species belonged to the order Hymenoptera (table S2, pt. A). Plant species belonged to six different families (table S2, pt. B).

In the historical dataset, we lack information regarding the elevation at which interactions were observed. However, it is probable that the majority of these observations were conducted in the vicinity of the Alpine Laboratory, at an elevation of 2,600 m. During the data resampling, we likely captured a broader range of elevations than in the original study. The elevation at which an observation is made can significantly influence our interpretation of phenological shifts, as phenology tends to be delayed at higher elevations compared with lower ones (Inouye and Wielgolaski 2024). To address potential biases stemming from differences in sampling elevation across time periods, we included only observations in the present dataset that were made within ±300 m of elevation of the Alpine Laboratory's elevation (i.e., 2,300 to 2,900 m). Of the data collected in the present, 66.49% fell into this elevation range (see fig. S3 for a histogram of observations). Furthermore, while the past dataset contained information on day and month of observation, information on the year of observation was often incomplete. Therefore, we pooled all observations per time period.

Statistical Analyses

We performed all statistical analyses using R statistical software (ver. 4.4.1; R Core Team 2024). Figures were produced using the R packages ggplot2 (ver. 3.5.1; Wickham 2016) and cowplot (ver. 1.1.3; Wilke 2024).

Phenological Change. To investigate the magnitude of phenological shifts in plant and pollinator communities across two time periods, we calculated onset, central tendency, end, and duration of flowering and flight for each plant and pollinator species in each period using two different approaches. First, we computed the earliest day of observation (onset), the mean day where flowers or pollinators were observed (mean), and the latest day of observation (end). Duration of flowering and flight was calculated as the difference between the end and onset of flowering or flight (hereafter referred to as the MinMax approach). This approach considers extreme events, which can be informative for detecting the impacts of climatic extremes that push phenology beyond typical bounds. However, considering extreme cases might be sensitive to outliers or sampling biases across the time periods. Therefore, we also used a percentile approach, which reflects relative positions of values in the dataset rather than extreme cases. Specifically, we fit phenological density distributions for each species in each period and derived the 5th percentile (onset), 50th percentile (median), and 95th percentile (end) from the cumulative distribution function. Duration was calculated as the range between the 95th and 5th percentiles. We present the results obtained by the percentile-based method in the supplemental PDF.

For both MinMax and percentile-based metrics, we then averaged and estimated standard errors of the metrics across species to assess overall phenological shifts in plant and pollinator communities. Subsequently, we ran Welch two-sample *t*-tests to compare the means between the historical and contemporary data and between plants and pollinators. To visualize phenological shifts in individual plant and pollinator species, we plotted density curves for species observations in each time period. We then performed a series of Welch two-sample *t*-tests based on the data to assess whether the mean day of observation for the species differed significantly between the periods.

Does Change in Overlap of Interacting Species Predict Persistence of Interactions? For all unique interactions between plants and pollinators meeting our criteria, we calculated the interaction persistence (binary; 1 if an interaction observed in the past persisted, 0 if the interaction was not observed in the contemporary dataset). Furthermore, we calculated change in days of overlap of interacting species between the time periods. Specifically, we calculated the number of days the plant and pollinator species involved in an interaction overlapped in each time period and then calculated the difference in days of overlap between the time periods. To investigate the relationship between interaction persistence and changes in temporal overlap, we performed a generalized linear mixed effects (GLME) model. Specifically, we fitted a binomial GLME model using the glmer function in the lme4 package (ver. 1.1.35.5; Bates et al. 2015). The model included interaction persistence as the response variable and change in days of overlap as the explanatory variable. To account for random variation attributable to individual species, we included random intercepts for both plant and pollinator species.

Results

How Did Phenology and Temporal Overlap of Plant and Pollinator Species Change across the Time Periods?

We examined changes in the community-wide mean onset, central tendency, end, and duration of flight and flowering activity between the historical and contemporary time periods. The results obtained by the two approaches (MinMax and percentile) were highly correlated (fig. S4) but yielded somewhat different results. Using the MinMax method, we found that the onset of pollinator flight activity occurred significantly earlier in the present compared with the past, by 10.76 days (~1.08 days per decade; table 1, pt. A; fig. 1*A*). Mean day, end, and duration of pollinator flight activity did not significantly differ across periods (table 1, pt. A; fig. 1*B*–1*D*). Using the percentile approach, we similarly found a significantly earlier onset of pollinator flight, by 13.23 days (~1.32 days per decade) and no significant differences in the median or end of flight activity (fig. S5; table S1). However, the observed earlier onset of pollinator flight resulted in a significantly longer flight duration in the present, by 11.9 days (~1.19 days per decade; fig. S5*D*; table S1). When considering individual pollinator

Table 1: Test statistics of Welch two-sample *t*-tests comparing metrics obtained from the MinMax approach for onset, mean, end, and duration in pollinator flight (pt. A) and plant flowering (pt. B) between two time periods

Variable	*t*	df	*P*	Mean past	Mean present	Difference in means
			A. Pollinators			
Onset	3.107	47.827	.003	165.8	155.04	−10.76
Mean	−1.823	47.957	.075	192.987	186.182	−6.804
End	.328	46.167	.744	214.4	212.92	−1.48
Duration	−1.635	47.634	.109	48.6	57.88	9.28
			B. Plants			
Onset	2.502	17.731	.022	178.9	161.3	−17.6
Mean	.628	16.507	.539	190.885	186.185	−4.699
End	−.554	15.573	.587	207.3	212.1	4.8
Duration	−2.738	16.861	.014	28.4	50.8	22.4

Note: All numbers are rounded to three digits.

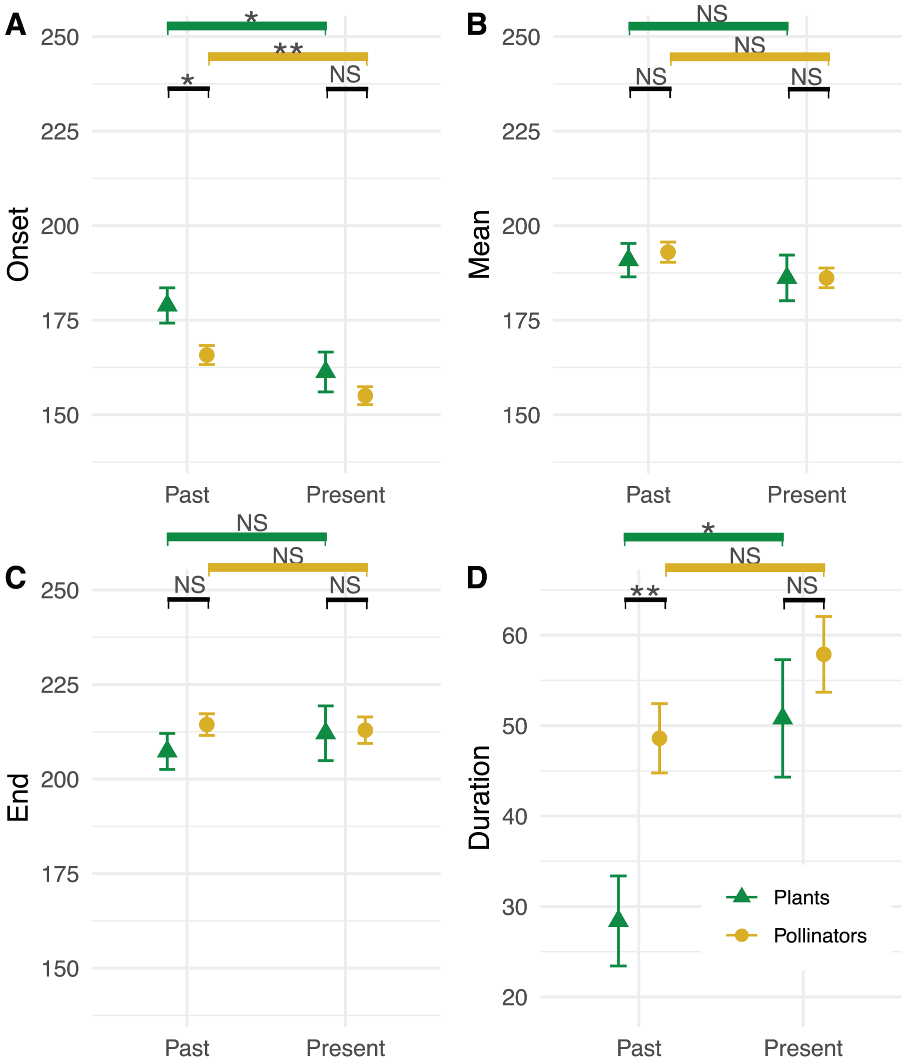

Figure 1: Distributions of plant flowering phenology and pollinator activity periods in past and present time periods. Point plots show the means and standard deviations of onset, mean, end, and duration of pollinator flight and plant flowering derived from the MinMax approach. Specifically, *A* depicts the earliest day of observation, *B* the mean day of observation, and *C* the last day of observation. *D* shows the difference between the end and onset. Asterisks indicate the significance level ($^{*}P < .05$, $^{**}P < .01$; NS = no statistically significant effect). Note that the *y*-axis scale in *D* differs from that of other panels.

species, we also detected significant differences in the mean day of activity (fig. 2). Of 25 pollinator species, 16 showed significantly earlier mean flight days, two showed significantly later mean flight days, and seven showed no significant patterns of shift (figs. 2, S6; table 2).

Regarding the plant community, we also found a significantly earlier onset in flowering using the MinMax approach, by 17.6 days (~1.76 days per decade; fig. 1*A*; table 1, pt. B). Mean and end day of flowering did not significantly differ (fig. 1*B*, 1*C*; table 1, pt. B), but duration of flowering was significantly longer in the present, by 22.4 days (~2.24 days per decade; fig. 1*D*; table 1, pt. B). Using the more conservative percentile approach, we could not confirm that the onset of flowering occurred significantly earlier in the present than in the past, and we also detected no significant shifts in median, end, or duration of flowering (table S1, pt. B; fig. S5). On a species level, in six of 10 plant species the mean flowering day occurred significantly earlier in the present and in three species it occurred significantly later in the present, while one species showed no significant shift between the time periods (figs. 3, S6).

To assess the temporal overlap between plant flowering and pollinator flight, we compared whether the plants and pollinators in each time period significantly differed in the mean onset, central tendency, end, and duration of flowering and flight. Using the MinMax approach, we found that

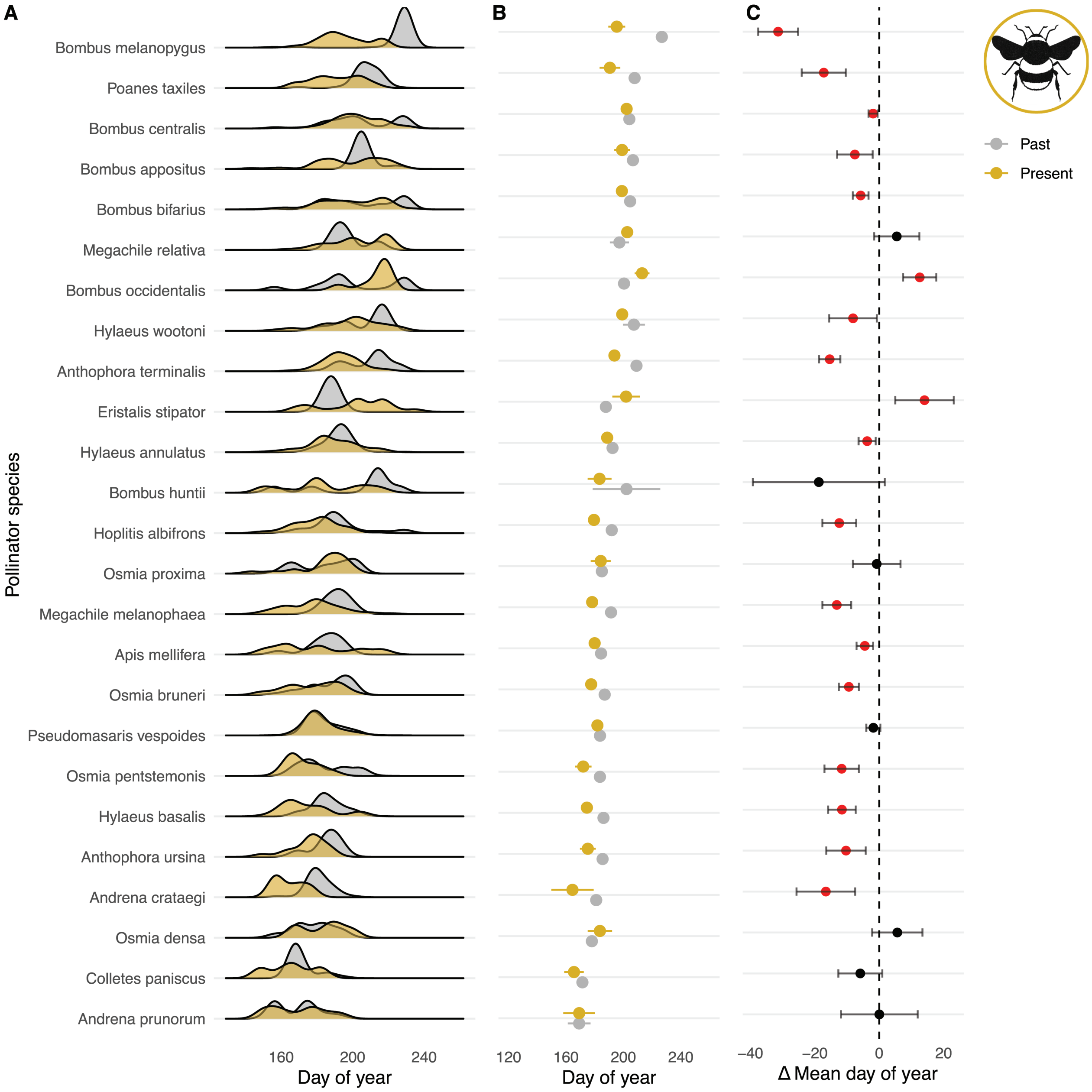

Figure 2: Phenological shifts in pollinator species. *A*, Density curves of Julian date for species observed in the past and present. *B*, Mean day of activity of a species and 95% confidence intervals for the past and present. *C*, Difference in mean day of activity of a species between the past and present, with 95% confidence intervals. Differences in species' mean day of activity in the past and present were tested using *t*-tests. Red points and confidence intervals not overlapping zero represent a significant difference in mean day of activity, while black points and confidence intervals overlapping zero indicate no significant difference.

in the past onset of flight and flowering differed significantly, with the onset of flowering being on average 13.1 days earlier than the onset of flight (~1.31 days per decade; table 3, pt. A; fig. 1*A*). The duration of flowering and flight in the past also differed significantly, where pollinator flight lasted on average 20.2 days longer than plant flowering (~2.02 days per decade; table 3, pt. A; fig. 1*D*). In the present, we found no significant differences in the onset, mean, end, or duration of flight and flowering (table 3, pt. B; fig. 1), which suggests that phenological shifts have increased synchronization between the average plant flowering period and the average pollinator activity period. Using the percentile

Table 2: Test statistics of Welch two-sample *t*-tests comparing mean day of pollinator flight (pt. A) and plant flowering (pt. B) across two time periods

Species	*t*	df	*P*	Mean past	Mean present	Difference in means
			A. Pollinators			
Andrena crataegi	3.568	3.038	.037	181.062	164.5	−16.562
Andrena prunorum	−.005	17.189	.996	169.167	169.2	.033
Anthophora terminalis	9.123	93.838	<.001	209.106	193.737	−15.369
Anthophora ursina	3.305	27.436	.003	185.5	175.188	−10.312
Apis mellifera	3.398	322.272	.001	184.426	179.959	−4.467
Bombus appositus	2.682	58.469	.009	206.64	199.08	−7.56
Bombus bifarius	4.612	900.597	<.001	204.68	198.922	−5.758
Bombus centralis	2.635	2,156.53	.008	204.131	202.231	−1.9
Bombus huntii	1.795	8.256	.109	202.143	183.393	−18.75
Bombus melanopygus	9.932	34.952	<.001	226.761	195.375	−31.386
Bombus occidentalis	−4.792	19.650	<.001	200.424	213	12.576
Colletes paniscus	1.689	20.715	.106	171.433	165.563	−5.87
Eristalis stipator	−3.033	18.732	.007	187.778	201.833	14.055
Hoplitis albifrons	4.624	105.241	<.001	191.87	179.475	−12.395
Hylaeus annulatus	2.763	139.374	.007	192.424	188.681	−3.743
Hylaeus basalis	5.293	70.082	<.001	186.13	174.558	−11.572
Hylaeus wootoni	2.152	16.697	.046	207.286	199.159	−8.127
Megachile melanophaea	5.781	74.309	<.001	191.383	178.214	−13.169
Megachile relativa	−1.522	19.044	.144	197.2	202.644	5.444
Osmia bruneri	5.937	211.574	<.001	186.957	177.533	−9.424
Osmia densa	−1.410	12.122	.184	178.024	183.636	5.612
Osmia pentstemonis	4.274	12.835	.001	183.65	172	−11.65
Osmia proxima	.208	30.483	.836	184.987	184.2	−.787
Poanes taxiles	4.930	18.152	<.001	207.796	190.588	−17.208
Pseudomasaris vespoides	1.634	119.201	.105	181.062	164.5	−16.562
			B. Plants			
Rubus deliciosus	3.105	1,175.857	.002	170.148	168.427	−1.721
Rubus idaeus var. *strigosus*	3.116	1,101.812	.002	186.461	185.617	−.844
Penstemon glaber	−3.224	1,430.764	.001	187.315	188.861	1.546
Penstemon secundiflorus	20.055	9.4	<.001	183.38	151.667	−31.713
Aquilegia coerulea	6.422	23.52	<.001	194.472	180.292	−14.18
Geranium richardsonii	−.651	161.074	.516	191.253	192.288	1.035
Geranium caespitosum	−5.566	2,343.245	<.001	198.807	202.495	3.688
Chamaenerion angustifolium	7.046	1,498.612	<.001	215.405	211.389	−4.016
Penstemon virens	3.965	546.801	<.001	173.941	170.929	−3.012
Aconitum columbianum	−3.291	16.736	.004	207.667	209.887	2.22

Note: All numbers are rounded to three digits.

approach, we did not find that the onset of flowering and flight differed from each other in either time period (fig. S5*A*; table S2). However, we detected that in the present, the duration of pollinator flight was significantly longer than plant flowering, by 18.6 days (~1.86 days per decade; fig. S5*D*; table S2).

Does Change in Overlap of Interacting Species Predict Persistence of Interactions?

We identified a total of 149 unique interactions within the subset of selected plant and pollinator species at our site. Of these, 28 interactions were observed exclusively in the present and 49 were observed only in the past. However, the apparent gain of interactions might not be as meaningful as the interaction losses, as we likely had a higher sampling effort in the present compared with the past and the gain of interaction may therefore be a sampling artifact rather than a real effect. Of the 149 unique interactions, 119 showed a greater temporal overlap in the present than in the past, 28 showed a lower temporal overlap in the present than in the past, and two showed no change in temporal overlap (table S3). To investigate whether the change in days of overlap between

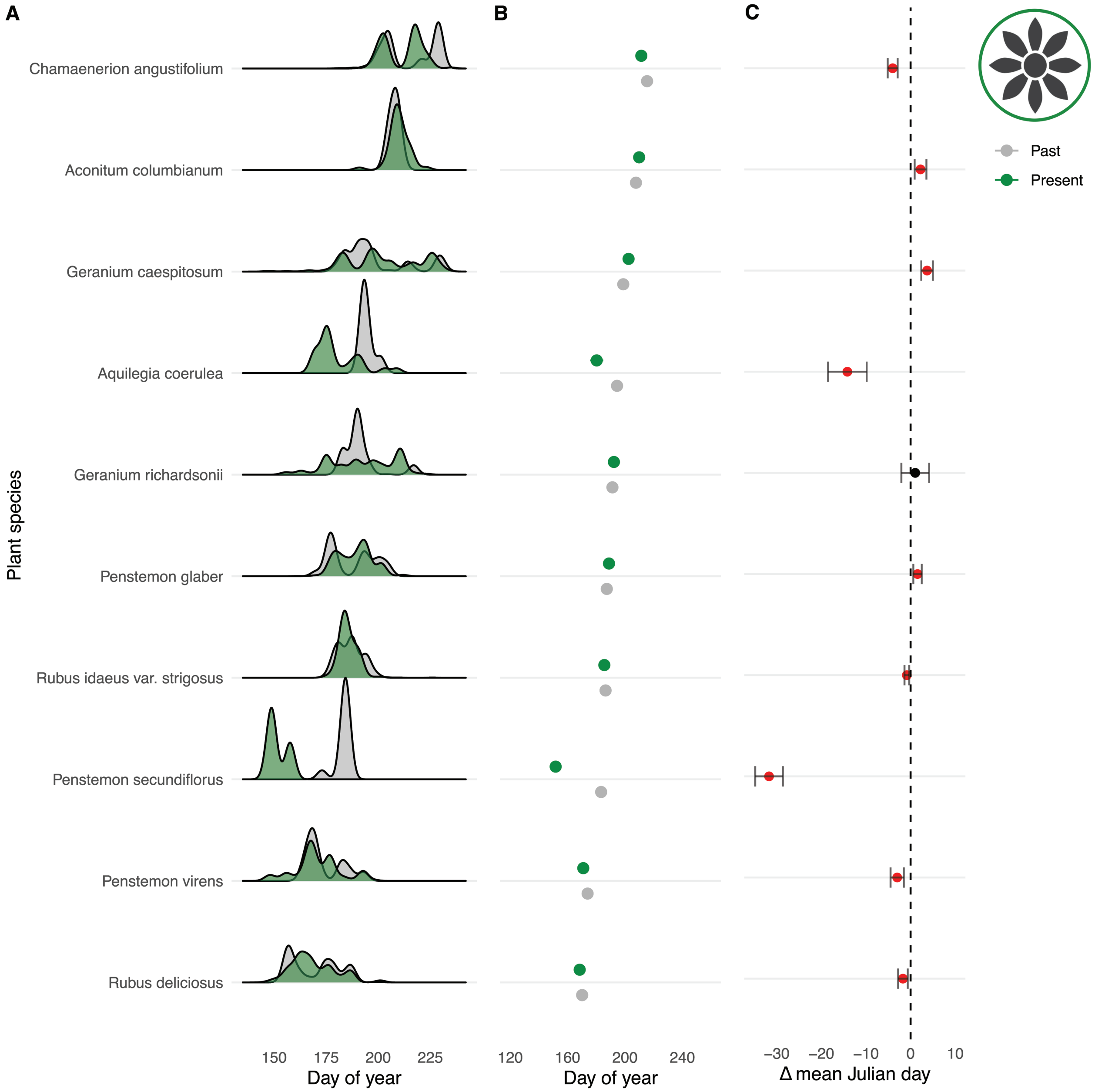

Figure 3: Phenological shifts in plant species. *A*, Density curves of Julian date for species observed in the past and present. *B*, Mean day of activity of a species and 95% confidence intervals for the past and present. *C*, Difference in mean day of activity of a species between the past and present, with 95% confidence intervals. Differences in species' mean day of activity in the past and present were tested using *t*-tests. Red points and confidence intervals not overlapping zero represent a significant difference in mean day of activity, while black points and confidence intervals overlapping zero indicate no significant difference.

two species predicted the persistence of their interaction across time periods, we fitted a binomial GLME model. The model revealed a significant positive relationship between the change in days of overlap and the probability of interaction persistence (estimate $= 0.042$, SE $= 0.021$, $z = 1.970$, $P = .049$; fig. 4). This result indicates that a larger overlap between plant and pollinator species corresponds to a higher probability that their interactions persist over time.

Discussion

In this study, we leveraged a unique historical dataset of plant-pollinator interactions recorded more than a century

Table 3: Test statistics of Welch two-sample *t*-tests comparing the metrics obtained from the MinMax approach for onset, mean, end, and duration of plants and pollinators between two time periods past (pt. A) and present (pt. B)

Variable	*t*	df	*P*	Mean plants	Mean pollinators	Difference in means
			A. Past			
Onset	2.473	14.576	.026	178.9	165.8	−13.1
Mean	−.406	15.995	.69	190.885	192.987	2.102
End	−1.278	15.858	.22	207.3	214.4	7.1
Duration	−3.216	20.188	.004	28.4	48.6	20.2
			B. Present			
Onset	1.083	12.821	.299	161.3	155.04	−6.26
Mean	.001	12.485	.999	186.185	186.182	−.003
End	−.102	13.417	.920	212.1	212.92	.82
Duration	−.917	16.94	.372	50.8	57.88	7.08

Note: All numbers are rounded to three digits.

ago and compared it with contemporary data to assess shifts in phenology and their effects on the persistence of interactions. We found significant shifts in pollinator phenology, with pollinators now flying earlier compared with the past. We also found evidence for plants flowering significantly earlier in the present compared with the past. Duration of pollinator activity was generally longer than duration of plant flowering, and pollinator flight and plant flowering periods were generally longer in the present than in the past; however, these results differed with the methodology used. When considering individual species, we found that six of 10 plant species and 16 of 25 pollinator species

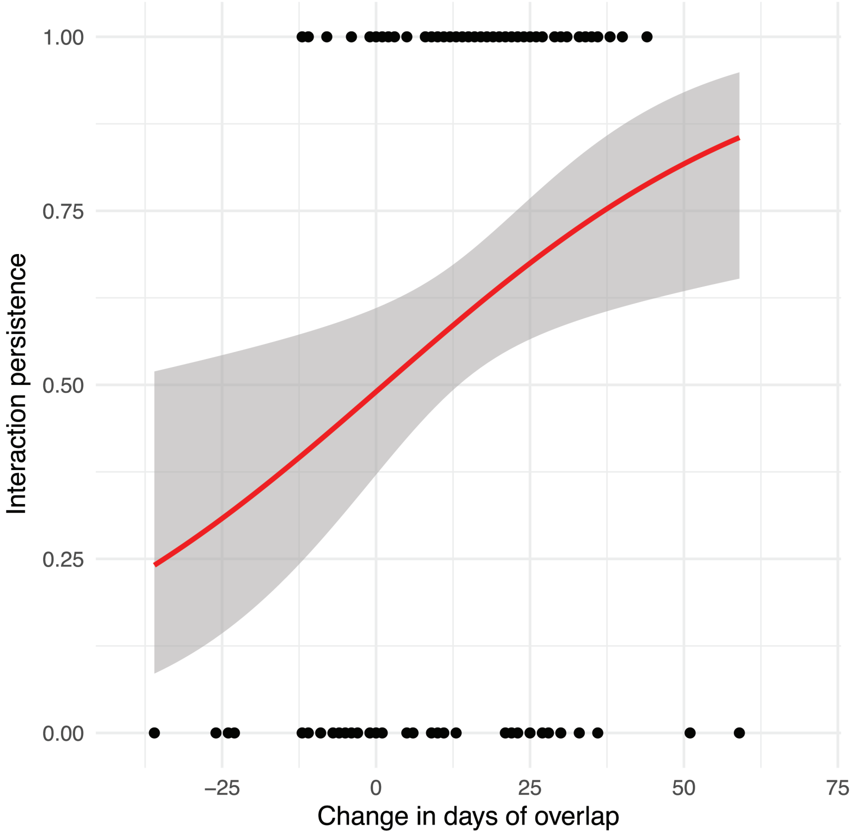

Figure 4: Predicted probabilities of interaction persistence across time periods as a function of change in days of overlap of interaction partners. The gray area indicates the 95% confidence interval of the predictions.

had a significantly earlier mean flight or flowering date in the present, emphasizing the broad taxonomic extent of the phenological shifts. Given these shifts in plant and pollinator phenology, we observed a greater temporal overlap between interacting species in the present, which in turn predicted a higher probability of the persistence of their interaction.

Our findings on the earlier onset of both plant flowering and pollinator flight are consistent with reports from other regions and across various taxonomic groups. For instance, Blasi et al. (2023) reported that the springtime activity of bumblebee queens in an agriculture-dominated landscape in Sweden has advanced by an average of 14 days over the past century. Similarly, Forister and Shapiro (2003) documented an average advancement of 1.7 days per decade in the peak flight times of butterflies in California. In England, Graham-Taylor et al. (2009) observed significantly earlier springtime appearances of several hoverfly species over a 17-year period. In the subalpine meadows of the Rocky Mountains, CaraDonna et al. (2014) found that while there was a general advancement in flowering onset over 39 years, species-level shifts were complex, with onset, peak, and last flowering rarely shifting uniformly.

Our study also provides evidence for increasing temporal overlap between plants and pollinators in the present, a trend that has also been observed in other regions (Inouye and Wielgolaski 2024). Similar to our results, Freimuth et al. (2022) reported that plant flowering in Germany historically started later than pollinator flight. However, the phenology of plants has generally advanced more rapidly than that of pollinators, leading to greater synchrony in the onset and duration of plant flowering and pollinator flight in the present. This increased temporal overlap between interaction partners is crucial for the persistence of plant-pollinator interactions over time. However, if the current trends continue, we may see a future where the timing of plant flowering and pollinator flight becomes more asynchronous again, albeit in different directions (i.e., plants flowering earlier than pollinators become active). The ecological consequences of such a shift remain uncertain, particularly in terms of how it might affect plant and insect communities and the overall stability of plant-pollinator networks.

Notably, one of the pollinator species that exhibited a significant delay in flight onset was the western bumble bee (*Bombus occidentalis*), a species whose distribution and abundance have sharply declined in recent decades (Cameron et al. 2011; Graves et al. 2020). The fungal gut parasite *Nosema bombi* (Microsporidia) has been identified as a factor contributing to these declines (Colla et al. 2006), likely acting synergistically with other stressors (Goulson et al. 2015; Cameron and Sadd 2020). Our findings suggest that disrupted interactions due to phenological shifts may be one such contributing factor. Alternatively, the reduction in *B. occidentalis* abundance over time (15 individuals recorded over 4 days in the present compared with 460 over 26 days in the historical period) likely disrupts interactions, as lower pollinator abundance inherently limits interaction opportunities. In our dataset, we recorded *B. occidentalis* interacting with six plant species. Four of the interacting pairs have declined substantially in temporal overlap, including three of the historically most frequent interactions for *B. occidentalis* (table S5). These results highlight the importance of considering phenological shifts in conservation efforts for declining pollinator species. Hence, restoration efforts should aim at preserving not only habitat and resources but also the temporal alignment of key plant-pollinator interactions to mitigate further disruption.

Many studies investigating phenological shifts report correlations among warming temperatures, timing of snowmelt, and phenological advancement (e.g., CaraDonna et al. 2014; Song et al. 2020; Freimuth et al. 2022), suggesting a causal link between climate change and phenological shifts. Furthermore, previous studies conducted in the Colorado Rocky Mountains have been able to directly link warming temperatures and earlier snowmelt to phenological changes (Dunne et al. 2003; Inouye 2008, CaraDonna et al. 2014). Our study did not directly investigate the relationship between temperature and timing of snowmelt changes and phenological shifts, as we were limited by a lack of historical records on temperature and timing of snowmelt to link with historical observations. Nevertheless, our observed patterns are likely influenced by warming temperatures and earlier snowmelt, as other potential factors, such as changes in land use or precipitation, were limited at our study site (Bolinger et al. 2024). It is important to also acknowledge that our study region is subject to substantial interannual variation in weather conditions, and the limited years of data representing both the historical period and the contemporary period may not fully capture climatic trends and their influence on phenological patterns. While historical resampling data are valuable for understanding these changes, they are not a perfect substitute for long-term monitoring datasets.

There are a variety of metrics used to estimate phenological changes, and the selection of the metric can have substantial impacts on the results (Moussus et al. 2010; Iler et al 2021). In this study, we used two approaches to estimate phenological events of plants and pollinators: the MinMax approach, which captures extreme events, and the percentile approach, which considers percentiles rather than extremes. The percentile approach is more conservative than the MinMax approach; hence, this approach resulted in the estimated onset of plant flowering and pollinator activity being later in the year compared with the estimates derived from the MinMax approach. Similarly, estimates of the end of flowering and flight activity were earlier in the year using the percentile approach. This in turn impacted the estimates of duration of flowering and flight between the two methods, therefore leading to some contrasting results. The MinMax method captures extremes, which can be crucial for understanding immediate ecological impacts, such as potential mismatches between plants and their pollinators, especially because extreme events become more common with climate change. But solely relying on this method might exaggerate the extent of phenological change in response to rare events, while the percentile method may better reflect long-term shifts in the phenology.

Despite the increasing use of historical data and museum collections to investigate phenological changes in plants and insects over extended time periods (Primack et al. 2023; Zhu and Song 2023; Rondinel-Mendoza et al. 2024), these approaches have a much greater potential. However, the increasing accessibility and integration of diverse historical data sources present a promising avenue for addressing pressing questions regarding the long-term impacts of anthropogenic change on ecosystems (Rakosy et al. 2022). Our study underscores the value of these historical datasets, highlighting their potential to reveal insights into the temporal dynamics of plant and pollinator species and their interactions. In the face of accelerating anthropogenic change, it is imperative to harness the wealth of information stored in historical studies and natural history collections to inform conservation strategies and ensure the persistence of these vital ecological interactions.

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Statement of Authorship

L.Z., J.R., and D.P.V. conceived the ideas. J.R. acquired the funding and led the data collection. L.Z. led the formal analysis and visualization of the data. L.Z. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data and Code Availability

All data and code used for generating the results are available on Figshare (https://doi.org/10.6084/m9.figshare.26950537; Zoller et al. 2025*a*) and GitHub (archived via Zenodo; https://doi.org/10.5281/zenodo.15627878; Zoller et al. 2025*b*).

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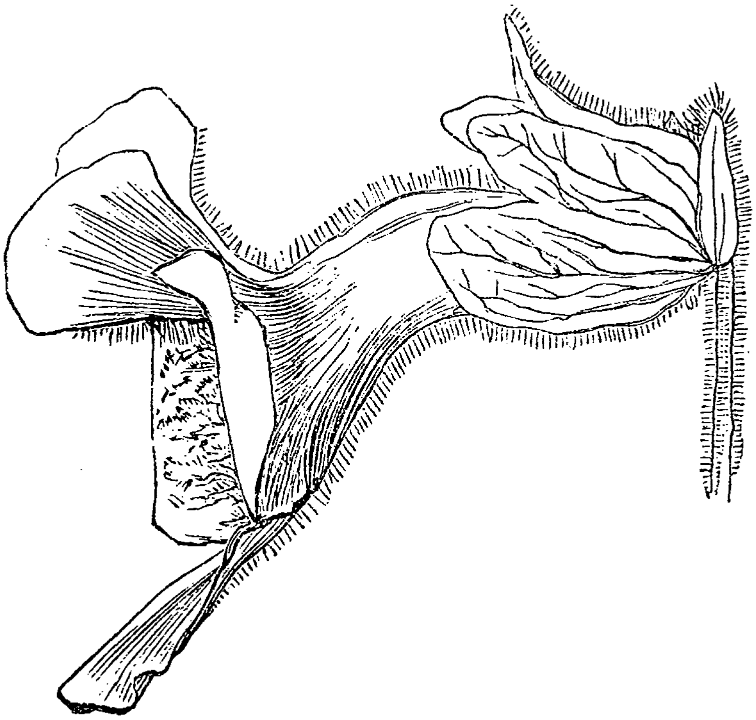

"Strangely enough many *irregular monopetalous* corollas seem to copy this *regular polypetalous* one in its method of cross-fertilization. This is especially true of *Martynia proboscidea* Glox., the unicorn plant." From "On Certain Contrivances for Cross-Fertilization in Flowers" by J. E. Todd (*The American Naturalist*, 1879, 13:1–6).