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Research

Long-term changes in flowering synchrony reflect climatic changes across an elevational gradient

EDITOR'S CHOICE

Alessandro Fisogni*, Natasha de Manincor*, C. David Bertelsen and Nicole E. Rafferty

A. Fisogni (https://orcid.org/0000-0001-6179-2767) ✉ (a.fisogni@gmail.com), N. de Manincor (https://orcid.org/0000-0001-9696-125X) and N. E. Rafferty (https://orcid.org/0000-0002-6350-1705) ✉ (rafferty@ucr.edu), Dept of Evolution, Ecology and Organismal Biology, Univ. of California, Riverside, CA, USA. – C. D. Bertelsen, School of Natural Resources and the Environment, Univ. of Arizona, Tucson, AZ, USA and Herbarium, Univ. of Arizona, Tucson, AZ, USA. NER also at: Rocky Mountain Biological Laboratory, Crested Butte, CO, USA.

Synchrony defines an organism's overlap with potential resources and mates, essential for survival and reproduction. Flowering synchrony influences gene flow within species and patterns of interaction among plants and with other trophic levels, including pollinators. Climate-change driven shifts in plant phenology may disrupt plant–plant and plant–pollinator interactions, resulting in reshuffling of communities and altered ecosystem processes. We present a unique long-term metacommunity-wide study relating changes in flowering synchrony within and among species along an elevational gradient to changes in local climatic conditions. We apply a circular statistical method that estimates flowering phenology overlap between entire flowering distributions, overcoming limitations and biases of single indicators such as first and last flowering dates. We analyzed more than 300 000 flowering overlap estimates between 217 species in five plant communities across a 1267 m gradient over four decades (1984–2019) in the southwestern USA. We show that co-flowering synchrony significantly decreased in all plant communities, with a maximum of 28.1% of synchrony lost at the lowest elevations. Decreased synchrony was significantly negatively correlated with increasing temperatures recorded across the gradient. Reduced precipitation had locally-dependent effects and, in combination with warmer temperatures, accelerated the decrease in synchrony, especially at the lowest elevations. Flowering synchrony within plant species occurring in multiple communities increased between most community pairs, with a maximum increase of 30.5%, and at accelerated rates in recent years. The exception, likely associated with differences in topography, was a 5.6% decrease in synchrony between the two highest-elevation communities. Overall, increased synchrony within species occurring at multiple elevations indicates homogenization of flowering phenology across the gradient. These results show significant reshaping of flowering synchrony within and between plant communities in response to changing climate. Because plant phenology influences many ecological processes, such fundamental changes may have far-reaching and negative effects on ecosystem stability.

Keywords: climate change, flowering phenology, metacommunity, mountain ecosystems, pollination

Introduction

Recent climatic changes are affecting natural communities across taxa and habitats around the world (Allen et al. 2020), driving shifts in the timing of life history events (i.e. phenology) and in the phenological synchrony of interacting species (Ovaskainen et al. 2013, Thackeray et al. 2016, Kharouba et al. 2018, Roslin et al. 2021). Phenological synchrony is critical for survival and reproduction, and therefore fitness, as it defines the extent to which organisms overlap temporally with potential resources, antagonists, mutualists and mates (Ims 1990, Donnelly et al. 2011). In plants, flowering phenology is the result of a complex interplay between genetic pathways and several environmental factors, such as variation in air temperature, precipitation and day length (Ausín et al. 2005, Brearley et al. 2007, Lesica and Kittelson 2010, Wilczek et al. 2010, Moore and Lauenroth 2017). Differential phenological responses therefore reflect individual variation in responses to changing climatic variables, and ultimately determine the temporal patterns of flowering among species within communities or 'co-flowering synchrony' and among individuals within species or 'flowering synchrony' (Elzinga et al. 2007, Forrest and Miller-Rushing 2010), although the mechanisms driving variation in phenological shifts within and among taxa are rarely identified (Chmura et al. 2019).

Temporal and spatial patterns of synchrony both within communities and within species (hereafter (co-)flowering synchrony when referring to both) play a key role in determining the occurrence, type and strength of interactions within plant communities and between trophic levels. For animal-pollinated plants, the extent of co-flowering synchrony can affect the magnitude of plant–plant competition and facilitation for pollinator attraction (Rathcke 1983). For example, if plant species flower at the same time and rely on the same pollinators, competition for pollinator visits can result in reduced pollination success (Brown et al. 2002). In addition, for co-flowering species that share pollinators, heterospecific pollen transfer can reduce plant reproductive output (Morales and Traveset 2008). Alternatively, co-flowering can facilitate pollination success by increasing patch-level floral display size and attractiveness to pollinators (Moeller 2004, Hegland et al. 2009). In turn, competition and facilitation for pollination affect patterns of gene flow, ultimately affecting plant reproductive fitness (Pauw 2013, Ison et al. 2014, Gleiser et al. 2018, Bergamo et al. 2020, Rivest et al. 2021). For pollinators, the diversity of co-flowering species determines the availability of foraging resources throughout their flight activity period. Depending on the degree of dietary specialization, pollinators such as solitary bees may require pollen and nectar resources from diverse plant species in a period of only a few weeks to sustain themselves and to provision their offspring (Vaudo et al. 2015). Co-flowering synchrony thus affects the overlap between pollinator foraging and flowering phenology; diminished overlap can decrease the reproductive fitness of both plants, via reduced pollinator availability, and pollinators, via reduced

foraging resources (Rafferty and Ives 2012, Rafferty et al. 2016, Ogilvie and Forrest 2017, Schenk et al. 2018, Kudo and Cooper 2019). At the same time, asynchronous flowering can be important for sustaining pollinator populations with longer foraging seasons. In this case, sequential flowering of species in a community, which may be maintained by interspecific competition for pollination (Aizen and Vázquez 2006), can benefit both plant and pollinator fitness, and increased overlap would be expected to negatively affect both partners (Waser 1979). Indeed, changes in the degree of temporal co-occurrence between flowering and pollinator foraging can potentially initiate extinction cascades and drive negative effects on ecosystem functioning (Memmott et al. 2004, Brosi and Briggs 2013).

Worldwide, montane climates are experiencing elevation dependent warming (EDW), as warming rates vary across elevation bands (Pepin et al. 2015). Although patterns of EDW are not uniform and may differ among regions and seasons, EDW in combination with regional factors is expected to cause a global average increase of surface air temperatures in mountains of $0.3 \pm 0.2°C$ per decade until the mid-21st century, regardless of the climate scenario (IPCC 2018, Hock et al. 2019). Changes in precipitation patterns are more heterogeneous than temperature changes, both among and within mountain regions. Future projections indicate annual precipitation increases of up to 20% in several regions (e.g. Himalaya, eastern Africa, European Alps), and decreases in the Mediterranean and the southern Andes (Hartmann et al. 2013, Hock et al. 2019). Similarly, the intensity and frequency of extreme precipitation events are expected to vary by season and region.

Overall, there is an expected reduction in snowfall as a percent of total precipitation (Kapnick and Delworth 2013). Snowfall is projected to decrease at lower elevations in association with increased temperatures, whereas increased winter precipitation at higher elevations can lead to greater average snowfall (Kapnick and Delworth 2013, O'Gorman 2014). Temperature, precipitation regimes and timing of snowmelt are important cues for both plant (Cleland et al. 2006, 2007, Forrest and Miller-Rushing 2010) and pollinator (Kudo and Cooper 2019, Abarca and Spahn 2021) phenology.

Longitudinal studies across elevational gradients are therefore uniquely suited to assess spatio-temporal changes in flowering phenology of plant communities under different environmental and climatic conditions. In subalpine wildflower communities across a 400 m elevational gradient, flowering onset, peak and duration shifted in relation to multiple climatic factors in species-specific ways, leading to changes in co-flowering richness (Theobald et al. 2017). However, this study was relatively short-term, examining flowering data over six consecutive summers. In our montane study area in the southwestern United States, climatic changes have been correlated with community-level shifts in mean flowering times of subpopulations using an earlier, shorter-term version of the dataset we analyze here (Rafferty et al. 2020). However, studies of flowering synchrony are still missing. Herein, we present to our knowledge the first long-term

metacommunity-wide study examining changes in (co-)flowering synchrony along an elevational gradient, enabling us to explore how communities are responding to changes in local climatic conditions. In addition, no such studies have been conducted in arid or semi-arid ecosystems, despite the fact that these regions cover a large area of the globe (Kottek et al. 2006) and can contain high levels of biodiversity and endemism (Rahbek et al. 2019, McDonald et al. 2021). To better understand changes in this fundamental aspect of plant phenology, studies across different ecosystem types are needed, enabling better predictions of how climate change will restructure the ecological communities that provide important services, such as pollination.

Here we analyzed (co-)flowering synchrony of a unique long-term dataset including more than 300 000 estimates of flowering overlap between 217 plant species spanning four decades (1984–2019) along a 1267 m elevational gradient in the Santa Catalina Mountains, USA (Bertelsen 2018). We considered five consecutive elevation bands of approximately 1.6 km each (Fig. 1) that include plant communities with species showing different flowering patterns, ranging from unimodal to bimodal and continuous flowering, without a winter resting period (Bertelsen 2018, Rafferty et al. 2020). Using single indicators of flowering phenology such as first, peak and last flowering date can prove inaccurate if population sizes or sampling frequencies change over time (Miller-Rushing et al. 2008). Individually, these indicators also fail to capture the fact that shifts in different flowering phenophases can be positively correlated, and shifts in one phenophase can have downstream effects on the timing of later components (Pearse et al. 2017). Moreover, analyzing such indicators using linear statistics can misrepresent phenological patterns of non-resting communities, for example by incorrectly calculating mean flowering dates and underestimating phylogenetic signals (Staggemeier et al. 2020). Therefore, we estimated temporal changes in synchrony using species-level flowering phenology distributions of entire plant communities along the gradient, taking into account the circular (i.e. year-round rather than seasonally discrete) flowering patterns of plant species. We used local temperature and precipitation data to correlate changes between climatic variables and co-flowering synchrony. Our goal is to advance understanding of long-term phenological patterns based on entire species-level flowering distributions and the climatic drivers associated with them. Specifically, we tested the hypotheses that (co-)flowering synchrony has changed across the elevational gradient, both within and between species, and that changes in synchrony are correlated with climatic changes across the different elevations. We expected the greatest changes in co-flowering synchrony within low-elevation plant communities. Drawing from the 'seasonality hypothesis' formulated by Janzen (1967), we might expect that species at lower elevations may have narrower physiological tolerance than species at higher elevations, because of the lower yearly temperature fluctuations to which they are subjected in the study area. We predicted that increased warming can impose additional physiological stress to that already caused by the extreme desert temperatures, and that it might alter the temporal dispersion of flowering at the community level. We further predicted that flowering synchrony has increased for species distributed across the gradient in response to warming (Vitasse et al. 2018), resulting in faster development
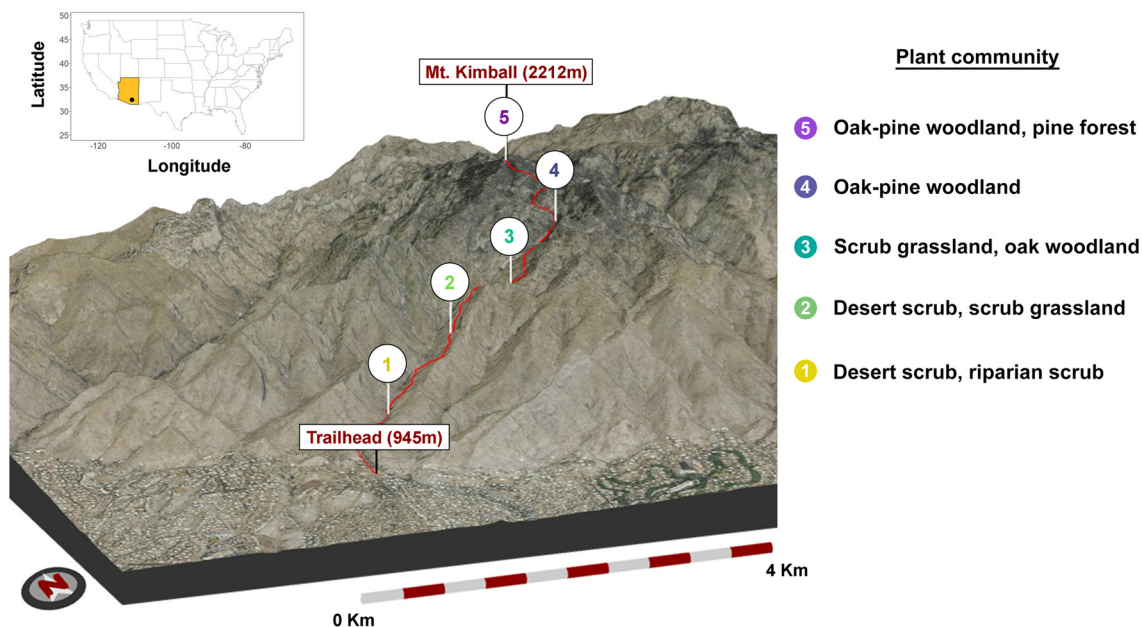

Figure 1. Map of the study site. The study site is located in the Santa Catalina Mountains, Arizona, USA. The transect (red line) along which plant flowering phenology was recorded from 1984 to 2019 is 8.05 km (5 miles) long and rises 1267 m in elevation, encompassing five different plant communities. Circled numbers indicate the end of each 1.6 km (1 mile) long transect segment, corresponding to five elevation bands.

(Carbognani et al. 2016), homogenization of flowering times within species (Zohner et al. 2018), and narrowing windows of opportunity for flowering at the individual level.

Methods

Study site and phenological data collection

This study was performed along a fixed transect of 8.05 km in length (5 miles) ranging from 945 m to 2212 m a.s.l. in the Santa Catalina Mountains near Tucson, Arizona, USA (Fig. 1). At the beginning of data collection the transect was divided into five consecutive elevation bands of approximately 1.6 km (1 mile) each (Fig. 1) that include five different plant communities ranging from desert scrub to pine forest (Fig. 1, Supporting information; for details see Crimmins et al. 2008, Bertelsen 2018).

One of the authors (CDB) systematically surveyed the transect at least twice monthly for 36 consecutive years from 1984 to 2019, except during 11 particularly cold or dry months when plants were dormant and except 2004–2005 and 2013 when regular surveys could not be conducted. Data were collected for an average of 32 days per year during the first nine years, a period of above-average precipitation, while data were collected almost weekly (56 days per year on average) from 1993 onward, when precipitation decreased to average and below average. During each survey, an area of about 9.1 m on each side of the transect was inspected, and flowering was recorded in each elevation band for all plant species and infraspecific taxa (hereafter referred to as species) presenting at least one flower in anthesis (angiosperms) or one cone releasing pollen (gymnosperms). Species were identified at the infraspecific rank when pertinent. Because of the large number of species observed, it was not possible to record quantitative data on flowering (e.g. number of individuals in bloom per surface area). If one individual was in anthesis the species was recorded as flowering, although each recorded observation usually included several flowers of a given taxon (Bertelsen 2018).

Phenology overlap estimates

Because we found that flowering occurred throughout the year at all elevations (Fig. 2), plant phenology is more accurately represented by circular than linear statistics (Staggemeier et al. 2020). Consequently, we quantified the extent of flowering phenology synchrony between pairs of species in a given year following the method proposed for activity data (here, presence of flowering at any given date) with a circular distribution and implemented in the R package *overlap* (Ridout and Linkie 2009). Dates of flowering are considered as a random sample from the underlying distribution that describes the probability of finding a species in flower at any particular day of the year. The probability density function of this flowering distribution presupposes that a plant is equally likely to be found at all times it is in flower. Then, a two-step process

to quantify the extent of overlap between the two flowering patterns of the species pair was performed. First, survey dates were converted to day of year (1–365 or 1–366 in leap years) and subsequently to radians, to consider year as a circular continuum and apply circular statistics (Staggemeier et al. 2020). Each flowering distribution was then estimated separately by fitting a non-parametric von Mises kernel density function. Unlike Gaussian kernels, von Mises kernels correspond to a circular distribution. Second, a measure of overlap between the two estimated distributions was calculated. The coefficient of overlapping (Δ) ranges from 0 (no overlap) to 1 (complete overlap), and corresponds to the area shared by the two functions being compared (Fig. 3). This method is well suited for our dataset, as it was developed for presence data with a circular distribution (Ridout and Linkie 2009), and fulfills the desirable characteristic for an overlap estimate of considering the perspective of both species together (Freitas and Bolmgren 2008). Following Ridout and Linkie (2009), we used two different overlapping estimators based on the size of the smaller of the two samples. We used Δ_1 when the smaller sample had less than 50 observations per year; otherwise we used estimator Δ_4. The estimators vary in the concentration parameter (c) of the kernel density, with $c=1.25$ for Δ_1 and $c=1$ for Δ_4 (Taylor 2008, Ridout and Linkie 2009).

We estimated the overlapping coefficients in two different ways to assess temporal and spatial variation in flowering phenology along the gradient: 1) co-flowering synchrony between all species pairs within each of the five elevation bands, 2) flowering synchrony within the same species across two or more elevation bands, considering two elevation bands at a time. To obtain a more robust and manageable data set, we included in the within-elevation band analysis the 217 species (36% of the 599 angiosperm and gymnosperm species in the study site flora) that flowered at least four times a year in each elevation band, and all species pairs that co-flowered for at least 10 years over a 20-year period across the entire 33-year study period. Since the number of species occurring in more than one elevation band was relatively low after filtering species that flowered at least four times a year at each elevation, we included all species pairs throughout the study period in the between-elevation bands analysis (Supporting information).

Climate data

Climate data was mainly retrieved from the parameter–elevation regressions on independent slopes model (PRISM) climate group database (Oregon State University, <http://prism.oregonstate.edu>, created 17 Sept 2020). Briefly, PRISM estimates gridded climatic parameters using point data, a digital elevation model and other spatial datasets allowing the slope of linear parameter–elevation relationships to change locally with elevation (Daly et al. 1994). Detailed cross-validation errors, prediction intervals, and comparisons with other spatial climate data sets are given in Daly et al. (2008). This type of climate data is especially well-suited for large elevation ranges where direct observations
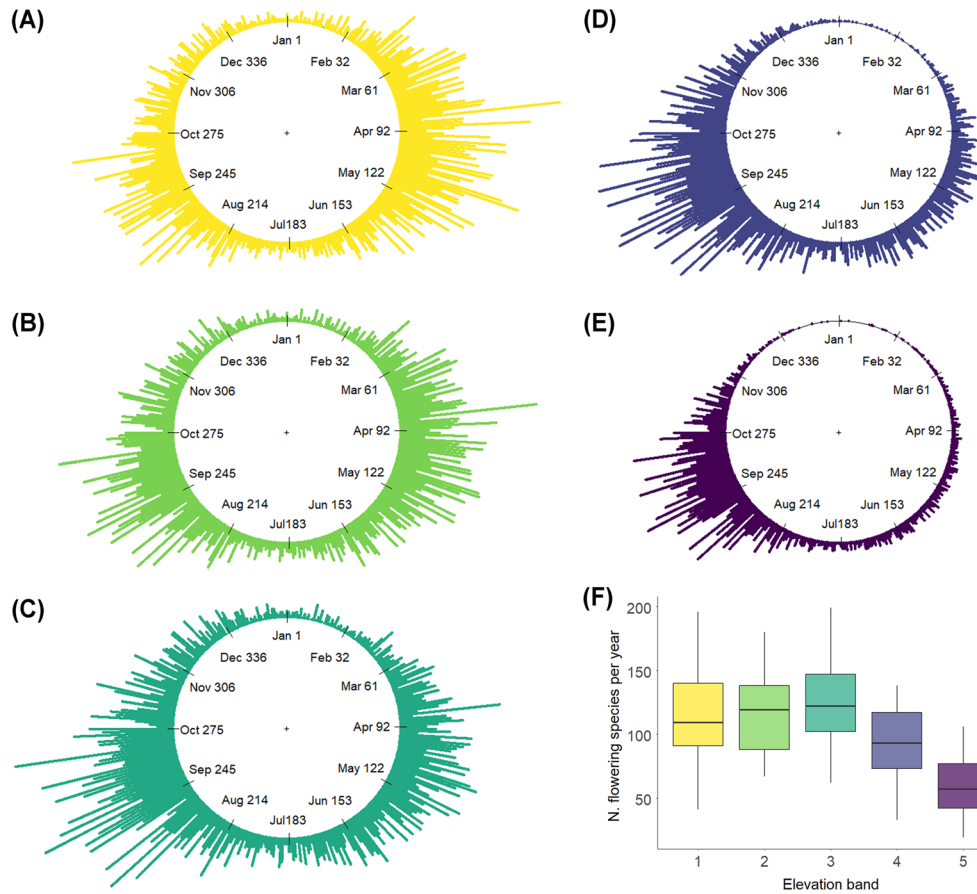
Figure 2. Flowering period (A–E) and number of flowering species (F) across the 33 years of study (within 1984–2019). Circular plots of elevation band 1: 945–1079 m (A), elevation band 2: 1079–1372 m (B), elevation band 3: 1372–1671 m (C), elevation band 4: 1671–1939 m (D), elevation band 5: 1939–2212 m a.s.l. (E). Bars in circular plots report the cumulative abundance of flowering for all species on any given date. Pooled across the 33 years of study, observations encompassed every day of the year. (F) Number of flowering species per year.

are lacking. Monthly precipitation from 1984 to 2006 and monthly average temperatures for the study duration were extracted from 800 m PRISM grid cells. From 2007 to 2019, precipitation was measured locally by means of rain gauges installed at 957 m (near the beginning of the transect), 1459 m (approximately halfway up the transect) and 2206 m a.s.l. (near the top of the transect) by one of the authors (CDB). Gauges were checked on average four times per month each year. Monthly data from the PRISM cells where rain gauges are located and data from the rain gauges are highly
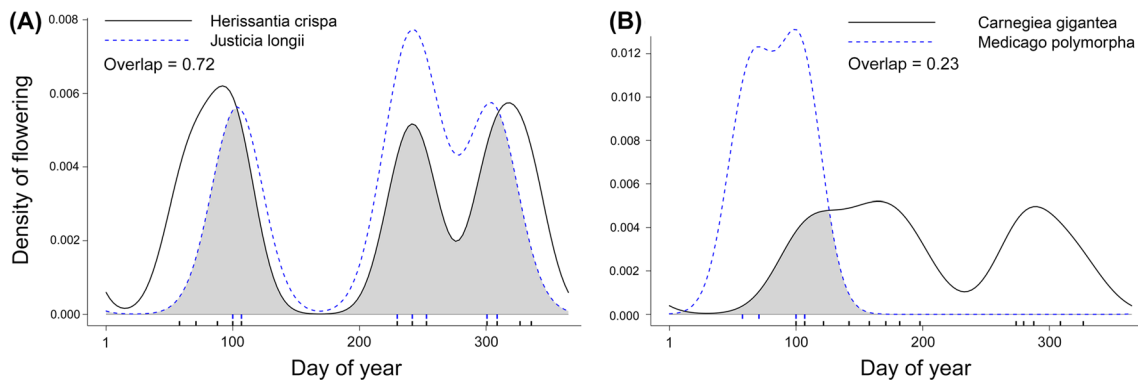

Figure 3. Example of kernel densities and overlap coefficients showing pairs of species with high (A) and low (B) flowering phenology overlap (shaded gray area). The overlapping coefficient ranges from 0 (no overlap) to 1 (complete overlap). The rug plots at the base of the fitted density curves show the actual flowering dates of each plant species throughout the year. Day of year 1 corresponds to January 1st.

correlated for each elevation (r = 0.81–0.87). Based on direct observation of long-term weather patterns, transect topography and local responses of vegetation to short-term climatic events, we used the low-elevation (957 m) temperature and precipitation data to explain overlap variation at the two lowest elevation bands, mid-elevation (1459 m) data to explain overlap variation at the intermediate elevation band, and the high-elevation (2206 m) data to explain overlap variation at the two highest elevation bands (Bertelsen 2018 and Rafferty et al. 2020 for details).

Data analysis

We excluded three years (2004, 2005 and 2013) from the analysis because irregular surveys occurred in those years (above). To evaluate temporal changes in flowering synchrony along the elevational gradient we fitted zero-and-one inflated beta regressions, since the overlapping coefficients are continuous proportions limited to, and including, 0 and 1 (Fang and Kong 2015, Douma and Weedon 2019). Beta regressions were fitted using Bayesian generalized linear mixed models with four Markov chain Monte Carlo (MCMC) chains with 10 000 iterations each (R package *brms*; Bürkner 2017). All models included the identity of species or species pairs as a random factor to account for repeated observations of species or pairs throughout the study period.

To evaluate changes in co-flowering synchrony along the altitudinal gradient across the 33-year study period, we first fitted a global model including all the overlapping coefficients estimated between species pairs within every elevation band as the response variable and year, elevation band and their interaction as predictors. In addition, we fitted the same model including the squared year predictor to allow for non-linear relationships. Then, we fitted two separate models for each of the five elevation bands including the overlapping coefficients as the response variable and either year or year squared as predictors. Year and year squared were scaled and centered around the mean in all models to allow better estimations and interpretation.

To evaluate how species occurring in any two elevation bands shifted their flowering synchrony through time, we fitted models between all pairs of elevation bands, including overlapping coefficients estimated for the same species at both elevation bands as the response variable, and year or year squared as predictors. Therefore, we obtained two models for each of the 10 elevation band pairs, for a total of 20 models. Models with linear and non-linear predictors (year and year squared, respectively) were compared using approximate leave-one-out (LOO) cross-validation (Vehtari et al. 2017).

To evaluate temporal changes in temperature and precipitation throughout the study period, we fitted separate linear regressions using log-transformed mean annual temperature and log-transformed total annual precipitation as response variables, respectively, and year, elevation and their interaction as predictors. The interaction in the model including temperature was significant; therefore we performed separate linear regressions for each elevation. For the model including precipitation the interaction was not significant; therefore we performed a linear mixed-effects model including elevation as a random factor to allow intercepts to vary by elevation (R package *lme4*, Bates et al. 2015). We then compared conditional and marginal R^2 values to evaluate if the model including the random effect explained more variance than the model including only the fixed effects (Nakagawa and Schielzeth 2013). Before regressing co-flowering synchrony to climatic predictors we checked for temporal autocorrelation in the three time series considered (i.e. synchrony, precipitation, temperature) using Ljung–Box tests with a lag of one year. Because we did not detect any significant autocorrelation (p > 0.05; Supporting information), we did not perform any detrending prior to analyses (Iler et al. 2017). To assess if temporal changes in co-flowering synchrony were related to climatic variables across the elevational gradient, we first fitted a zero-and-one augmented beta regression, as described above, including phenology overlap between all pairs of species within all elevation bands as the response variable and temperature, precipitation and their interaction as predictors. We then fitted separate models for elevation bands 1–2, elevation band 3 and elevation bands 4–5 with the respective climate parameters. All models included species pair as a random factor.

Results

Temporal reductions in within-community co-flowering synchrony

Co-flowering synchrony linearly decreased through time at all elevations, but at different rates across elevations (Fig. 4A, Supporting information). Co-flowering synchrony decreased by 28.1% at elevation band 1, by 15.4% at elevation band 2, by 13.7% at elevation band 3, by 9.2% at elevation band 4 and by 14.4% at elevation band 5 across the 33-years of study (Supporting information). We did not find any significant non-linear decrease of co-flowering synchrony over time. The lowest elevation band had the steepest decline in overlap, with values similar to elevation bands 4 and 5 at the beginning of the study and values similar to elevation bands 2 and 3 at the end of the study (Fig. 4A). Overall, co-flowering synchrony was always significantly higher at elevation bands 4 and 5 than at lower elevations throughout the study period (Fig. 4A).

Changes in between-community flowering synchrony

Flowering synchrony within the same species occurring across multiple elevations significantly differed between pairs of elevation bands, and showed a significant non-linear interaction between time and elevation band pair (Supporting information). Synchrony was higher between adjacent elevation bands, and decreased as the spatial separation along the gradient increased (Fig. 4B). Synchrony increased through time between all elevation band pairs except between elevation
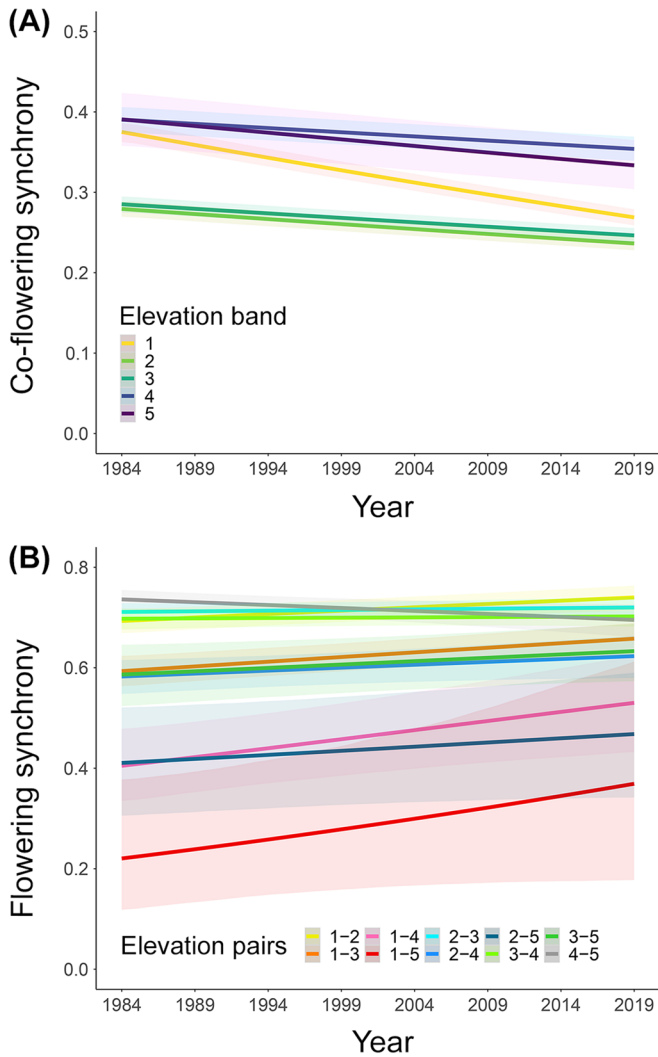
(A)

(B)

Figure 4. Temporal changes in (A) co-flowering (i.e. among species within elevation band) synchrony and (B) flowering (i.e. within species among pairs of elevation bands) synchrony estimated across the elevation gradient over 33 years (within 1984–2019). Elevation band 1: 945–1079 m, elevation band 2: 1079–1372 m, elevation band 3: 1372–1671 m, elevation band 4: 1671–1939 m, elevation band 5: 1939–2212 m a.s.l. Zero indicates complete asynchrony, 0.5 and 0.8 indicate 50% and 80% flowering synchrony, respectively.

bands 4 and 5 (Fig. 4B), in which it decreased in a non-linear fashion, resulting in a 5.6% loss of overlap over the 33 years of study (Supporting information). Flowering synchrony increased significantly and at non-linear rates between elevation bands 1–2, 1–3 and 1–4 resulting in a 6.8, 10.8 and 30.5% loss of overlap over 33 years, respectively (Fig. 4B; Supporting information).

Complex responses to climate change

Temporal changes in co-flowering synchrony were significantly correlated with changes in temperature and precipitation across the altitudinal gradient, with a significant

interaction between these climatic variables (Supporting information). Temperature significantly increased through time across the gradient ($F_{1,102}=98.56$, $p < 2.2e^{-16}$), with larger increases at higher elevations (Fig. 5A; elevation 1: $F_{1,34}=15.05$, $p=4.6e^{-04}$; elevation 2: $F_{1,34}=34.65$, $p=1.21e^{-06}$, elevation 3: $F_{1,34}=49.22$, $p=4.27e^{-08}$). Precipitation significantly decreased through time across the gradient ($F_{1,102}=41.58$, $p=3.822e^{-09}$), with similar decreases among elevations (Fig. 5B).

Increased temperatures were significantly correlated with decreased flowering synchrony at all elevations when holding precipitation constant, with stronger effects at elevation bands 4 and 5, while decreased precipitation was positively or negatively correlated with synchrony depending on the elevation when holding temperature constant (Supporting information). Temperature and precipitation had different interacting effects at different elevations. At the lowest elevation band, flowering synchrony was predicted to decrease more strongly with
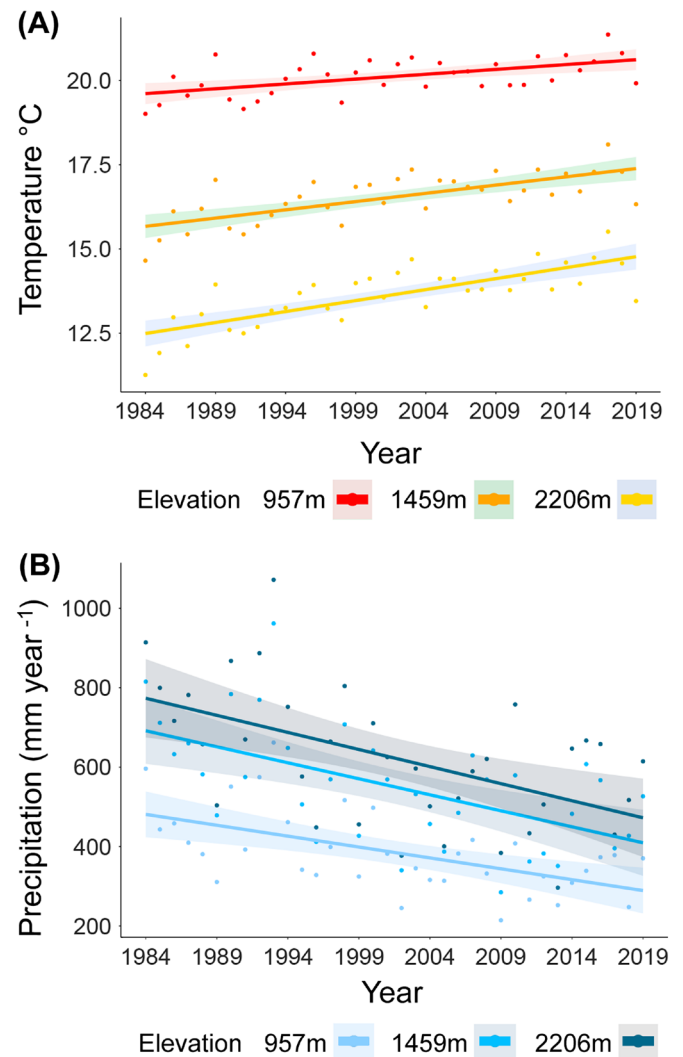
(A)

(B)

Figure 5. Temporal changes in mean annual temperature (A) and total annual precipitation (B) measured at three elevations from 1984 to 2019. Shaded areas represent 95% confidence intervals.

precipitation around or below the average levels as temperature increased through time (Fig. 6A). Changes in both temperature and precipitation were related to decreased synchrony through time at elevation band 2, with no significant interactions between them (Supporting information). At the intermediate elevation band 3, flowering synchrony was predicted to moderately decrease with below-average precipitation as temperature increased, while a stronger decrease in synchrony was predicted to occur with above-average precipitation (Fig. 6B). At elevation band 4, increased temperatures were generally related to decreased synchrony, slightly more so with precipitation around or below the average levels (Fig. 6C). At the highest elevation band, flowering synchrony moderately decreased with above-average precipitation as temperature increased, while below-average precipitation was predicted to decrease synchrony more steeply as temperature increased (Fig. 6D).

Discussion

The findings reported here demonstrate that climate change is restructuring ecological communities in profound ways. Changing conditions in temperature and precipitation across elevations are associated with large shifts in flowering synchrony both within species in different communities and among species in the same community over the last four decades. Because flowering synchrony affects gene flow (via pollen transfer among conspecifics), reproductive interference (via pollen transfer among heterospecifics) and competition as well as facilitation for pollination services, the reduced flowering phenology overlap observed will likely directly affect plant fitness (Ghazoul 2006, Morales and Traveset 2008, Ison et al. 2014, Gleiser et al. 2018, Hall et al. 2018, Kehrberger and Holzschuh 2019, Rivest et al. 2021). At the same time, reduced flower availability over time will likely affect pollinator fitness (Rundlöf et al. 2014, Kaluza et al. 2018, Schenk et al. 2018), and ultimately the consequences are likely to be felt throughout ecosystems as processes such as nutrient cycling are altered (Forrest and Miller-Rushing 2010, Delgado-Baquerizo et al. 2013, González de Andrés 2019).

Reductions in within-community co-flowering synchrony over time

Co-flowering synchrony significantly decreased within communities throughout the elevational gradient over the last
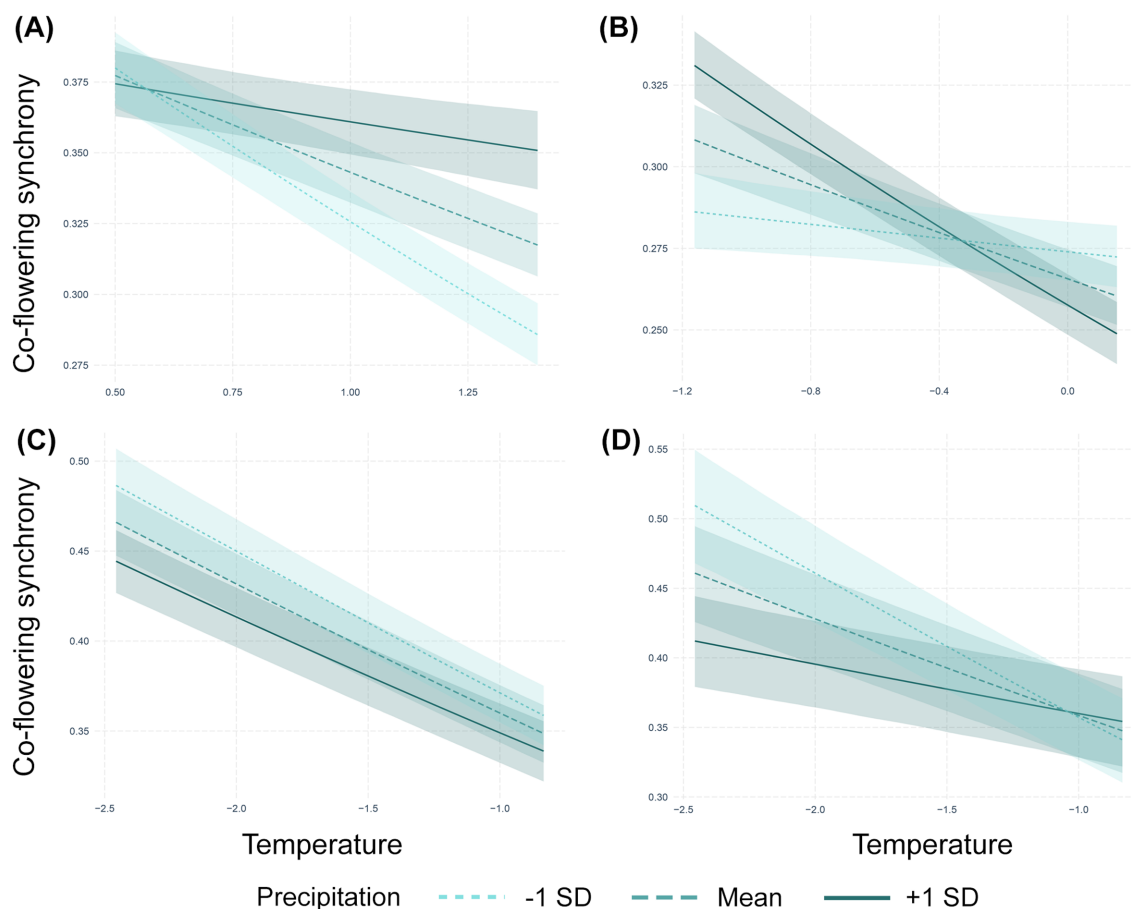

Figure 6. Interacting effects of temperature and precipitation on co-flowering synchrony in elevation band 1 (A), elevation band 3 (B), elevation band 4 (C) and elevation band 5 (D). Elevation band 2 did not show significant interactions. The effect of temperature is moderated by average, low (−1 SD of the mean) and high (+1 SD of the mean) precipitation. Temperature and precipitation are centered around the mean.

four decades, with the greatest reduction in synchrony within the community at the lowest elevations. The historical co-flowering synchrony among species observed along the gradient reflects the unique evolutionary history of each species (Wang et al. 2020), shaped by both abiotic and biotic factors, including selection pressures imposed by other species. The temporal changes observed in co-flowering synchrony within communities imply different inter-specific phenological responses to environmental factors, which mainly reflect differences in the sensitivity and phenological plasticity of species (Diez et al. 2012, Rice et al. 2021).

Reduced community-level co-flowering synchrony can decrease phenological overlap with pollinators as plant species that historically overlapped strongly in flowering phenology become more staggered in time. However, reduced co-flowering synchrony could also diminish gaps in the flowering season. Either scenario will be especially relevant for pollinators with short activity periods (Memmott et al. 2007, Rafferty et al. 2015, Ogilvie and Forrest 2017). These effects could be particularly pronounced for the lowest elevation community, where flowering synchrony decreased of almost a third (28.1%) over the study period. Such significant loss of flowering overlap could represent a large portion of the nesting and foraging period of solitary bees (Trostle and Torchio 1994, Bosch and Kemp 2000). For example, female *Osmia lignaria* and *O. cornuta* bees have a lifespan of 20 and 18–31 days, respectively, during which time a single female bee must visit tens of thousands of flowers of multiple species to collect adequate nectar and pollen to provision her offspring (Bosch and Kemp 2000, Bosch and Vicens 2006). From the plant perspective, reduced co-flowering synchrony could result in lower pollinator availability via phenological mismatch, reducing plant reproductive output (Rafferty and Ives 2012, Kehrberger and Holzschuh 2019, Richman et al. 2020), with potentially significant and long-lasting effects. Thus, shifts in co-flowering phenology could have negative and cascading effects on communities by altering plant–animal interactions. Plants could experience reduced pollination services leading to reduced seed set (Knight et al. 2005) which would support smaller communities of seed predators, further cascading to reduce seed dispersal and seedling recruitment (Wang and Smith 2002, Heleno et al. 2011, Carlo and Tewksbury 2014). Reduced co-flowering synchrony could reduce competition among plants for pollinators and resources, as well as reduce heterospecific pollen transfer within communities. However, these potentially positive effects can be counteracted by reduced facilitation via shared pollination attraction (Hegland et al. 2009).

At low elevations, where the greatest loss of synchrony occurred, plants likely have narrower thermal tolerances compared to high-elevation species (Janzen 1967, Sheldon et al. 2018). Therefore, increased temperatures at lower elevations may generate more extreme, stress-induced phenological responses, resulting in decreased synchrony among species (Richardson et al. 2013). Moreover, increased evapotranspiration associated with longer droughts and increased soil water deficit, which is enhanced by shallow lithic soils at low elevations in our study area (Whittaker et al. 1968), may have magnified the physiological stress induced by increased temperatures (Piao et al. 2019). The warming recorded in the study region in the last five decades (Zhang et al. 2021) is projected to continue into the future, with average increases of 2–4.8°C by the end of the 21st century under different global change scenarios (Vose et al. 2017). We expect that continued exposure to increasingly higher temperatures might induce further physiological stress and modify flowering phenological responses of plants occurring at all elevations (Collins et al. 2021), which in turn are likely to intensify the observed patterns of reduced synchrony within communities.

Within the highest-elevation communities, the relatively high overlap in flowering phenology (of ~ 40%) throughout the study period is consistent with the stress gradient hypothesis, suggesting that facilitation is more important at higher than at lower elevations (Bertness and Callaway 1994, Duarte et al. 2021). High co-flowering synchrony in these communities, where species richness is lowest and flowering is concentrated in the summer months, may facilitate pollinator attraction and pollination services (Bergamo et al. 2020), while at the same time reducing gaps in floral resource availability and sustaining pollinator populations (Elzinga et al. 2007, Venjakob et al. 2016). For high-elevation plant communities, temperature has historically been the greatest stressor, although the interaction between warmer winter temperatures and decreasing precipitation is becoming an important stressor, reducing snowpack and increasing evapotranspiration (Pepin et al. 2015, Bertelsen 2018, Winkler et al. 2019).

Changes in between-community flowering synchrony over time

Flowering synchrony within species occurring in different communities increased over time between all elevation pairs, except for the two highest elevations where synchrony decreased. In particular, we observed significant non-linear temporal responses when considering species that flowered at the lowest elevations and at elevation bands 2, 3 and 4, indicating that the trend of increasing flowering synchrony accelerated in more recent years. Species with highly conserved climatic niches can track climatic changes by advancing their flowering phenology, while species that are unable to maintain their climatic niche by shifting their phenology are more prone to range shifts (Amano et al. 2014). Our results suggest that climate warming has driven plant species occurring at higher elevations to advance their flowering faster than those at lower elevations, thereby reducing the phenological discrepancy between lower and higher elevations (Vitasse et al. 2018). Plants that advance flowering times with warming are more likely to maintain or increase their fitness, and can be subject to directional selection favoring earlier flowering (Manguía-Rosas et al. 2011, Anderson et al. 2012, Cleland et al. 2012). The non-linear responses observed at lower elevations are consistent with the accelerated advance in flowering phenology observed in the last decade at elevation bands 1–4 at our site (Rafferty et al. 2020), suggesting

that species with high phenological plasticity are responding to the increasingly stressful conditions at lower elevations.

The decrease in flowering synchrony over time observed in species occurring at the two higher communities was likely driven by the local topography. Elevation band 4 traverses a very steep slope with primarily northwestern exposure, while elevation band 5 traverses much less-steep slopes and includes exposures in all directions along the trail. In addition, band 4 has deeper soils with less-exposed bedrock and experiences greater cold air drainage and warm air rising than band 5. As a consequence, conspecific plants with local adaptations to different micro-climates could be affected in different ways by the similar climatic changes recorded at both elevations (Inouye 2008). Adaptation at this local scale may have driven divergent temporal shifts in flowering optima or induced shorter flowering periods for some species at the highest elevations, enlarging flowering gaps that resulted in reduced flowering synchrony between the two communities.

Complex responses to climate change

We found significant and complex responses of flowering synchrony to climatic changes in all plant communities across the elevational gradient. Temperature significantly increased along the gradient, with greater rates of increase at higher elevations, consistent with global trends of elevation-dependent warming observed across different mountain ranges (Pepin et al. 2015). Precipitation significantly and homogeneously decreased along the gradient. In contrast to temperature, no clear global trend in precipitation has been observed with locally varying responses in mountain areas (Kohler et al. 2014, Hock et al. 2019), although strong decreases in the amount and frequency of precipitation have been observed in the southwestern USA (Zhang et al. 2021). Our results suggest that temperature was the strongest driver of decreased co-flowering synchrony throughout the gradient. In particular, reduced synchrony in response to warming was strengthened by below-average precipitation at the lowest elevations, while it was strengthened by high precipitation at intermediate elevations. Synchrony was less dependent on precipitation at the two highest elevation bands. Although temperature is an important cue for plant phenology, variation in precipitation is often the main driver of flowering phenological patterns in arid environments (Forrest and Miller-Rushing 2010), which could explain the stronger impact of decreased precipitation on co-flowering synchrony at the lowest elevations, where a narrower range of temperature tolerance (Sheldon et al. 2018) means species may be further stressed by warming. The mid-elevation communities have experienced more dispersed flowering times in recent years (Rafferty et al. 2020), which likely reduced flowering synchrony. Higher elevations receive more precipitation and have much greater water storage capacity than lower elevations, because of deeper soils (elevation band 4) or highly fractured bedrock (elevation band 5), that may mitigate the effect of increasing temperatures through increased water availability. However, prolonged increasing temperature and decreasing precipitation likely increase plant competition for the reduced available subsurface moisture and nutrients, which could result in phenological shifts among species with different life history traits and rooting depths (Sherry et al. 2007, Dorji et al. 2013, Zhu et al. 2016). Moreover, the expected reduction in snowfall and earlier snowmelt due to climate warming (Kohler et al. 2014, Hock et al. 2019) could alter micro-climatic factors and drive significant changes in flowering phenology (Dunne et al. 2003, Iler et al. 2013, Theobald et al. 2017) and co-flowering synchrony (Carbognani et al. 2016) of plant communities at the higher elevations.

Limitations of the study

We estimated phenological overlap based on presence of flowering at any observation period. This use of presence data assumes that synchrony is proportional to the overlap between two species over time. However, floral abundance within species usually varies over time, and species may exhibit different levels of intra-population synchrony throughout their reproductive period. The use of abundance or frequency data would have allowed us to address finer temporal variation in flowering overlap. However, floral abundance estimates were not possible because of the large number of species occurring throughout the gradient and the extensive nature of the observations, both spatially and temporally. A loss in precision was compensated by the large scale of this study, which enabled insights into how changing climatic conditions have affected flowering patterns at the metacommunity level.

Because of the enormity of the dataset, we had to filter data to obtain a robust but analytically manageable number of field observations. To do so, we have excluded species that flowered sporadically throughout the sampling period, and focused on the phenological changes of the species that flowered more frequently. Nonetheless, the proportion of species considered in the final analysis of the initial number of species was comparable throughout the gradient (Supporting information). This indicates that data filtering did not alter species distributions among elevations, and suggests that our results give a correct representation of the core changes occurring across the study gradient.

Conclusions

Mountain ranges around the world have experienced similar warming patterns in the last decades. Our results show that increased temperatures are likely the main driver of reduced co-flowering synchrony in plant communities across elevations, and especially so for communities at the warmest and driest low elevations. As temperatures are predicted to continue to rise in the future in the southwestern United States (Vose et al. 2017), we can expect an exacerbation of these effects also at higher elevations. Although precipitation patterns are less generalizable

and can have different elevation-dependent interactive effects with temperature, increased precipitation variation, reduced snow fall and earlier snowmelt (Klos et al. 2014, Dannenberg et al. 2019) can be expected to intensify the observed patterns in the future. Reduced flowering synchrony can directly affect plant reproductive success, and cause cascading effects on interacting partners (e.g. pollinators, florivores, seed dispersers) and on the entire ecosystem, potentially decreasing functional redundancy and resource complementarity leading to altered ecological equilibriums (Blüthgen and Klein 2011, Brosi et al. 2017). Additional studies of changes in (co-)flowering synchrony across elevational gradients in other climatic regions are needed to better understand the global impacts of climatic changes on plant communities and ecosystems. In particular, the inclusion of data on biotic interactions among plants and their pollinators would allow the exploration of ecological consequences of altered competition, facilitation, resource use and ultimately fitness, and how they are related to changes in patterns of phenological overlap.

Author contributions

Alessandro Fisogni: Conceptualization (equal); Formal analysis (equal); Methodology (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Natasha de Manincor**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **C David Bertelsen**: Conceptualization (equal); Data curation (lead); Investigation (lead); Writing – review and editing (equal). **Nicole E. Rafferty**: Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.5586297> (Fisogni et al. 2021).

Supporting information

Any supporting information associated with this article is available from the online version.

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