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The Impacts of Climate Change on Plant-Pollinator Phenological Synchrony Along Climatic Gradients in Dryland Ecosystems

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The Impacts of Climate Change on Plant-Pollinator Phenological Synchrony Along Climatic
Gradients in Dryland Ecosystems

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Elijah Hall

December 2023

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Dedication

I dedicate this dissertation to the plants and animals of the White Mountains of
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Research Center and Santa Rose Mountains. I have learned so much thanks to them.

ABSTRACT OF THE DISSERTATION

The Impacts of Climate Change on Plant-Pollinator Phenology Along Climatic Gradients
in Dryland Ecosystems

by

Elijah Hall

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal Biology
University of California, Riverside, December 2023
Dr. Nicole E. Rafferty, Chairperson

Anthropogenic climate change represents one of the most serious threats to ecosystems in the 21st century. As temperatures increase, and precipitation patterns are altered, species need to respond to living in increasingly arid environments. The most noticeable responses to changing climate is for populations to shift spatially, typically upward in elevation and latitude, and phenologically, typically by becoming phenologically active earlier in the year. Variation in how individual organisms or populations respond to climate change can alter their ecological interactions. The timing of flowering is species specific, and when and with whom a plant flowers adjacent to can impact their reproductive success. Between trophic levels, the synchronous phenology of flowering plants and pollinators is critical for both plant and pollinator reproductive success. Plant-plant and plant-pollinator phenological synchrony is at risk of deterioration due to aridification, potentially decreasing ecosystem functioning across the globe. While the bulk of previous research on this issue has been conducted in humid systems, plant-pollinator phenological synchrony has been in understudied in dryland ecosystems, which

encompass over 40% of land globally. In the following chapters, I leverage natural history data along spatial and temporal gradients to determine the impacts of climatic variation on plant-plant and plant-pollinator phenological synchrony. I find evidence that plant-plant phenological synchrony is sensitive to changes in community composition. Plant-pollinator phenological synchrony decreases with increasing aridity at the community level, but some species are better suited to future aridification than others. My dissertation highlights the importance of understanding phenological synchrony in dryland ecosystems using analytical techniques specifically suited to the stochastic nature of climate change in these systems.

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Introduction

Climate change is altering the ecology of all species on Earth (Pörtner & Farrell 2008; Kiers et al. 2010). In particular, changing temperature and precipitation patterns are causing species to shift where (Parmesan et al. 1999; Madsen-Hepp et al. 2023) and when (Cohen et al. 2018; Vitasse et al. 2022) they exist. Species, and individuals within species, have specific phenological triggers in response to patterns of temperature and precipitation (Ollerton & Lack 1992). Not all species respond the same to shifts in temperature and precipitation, leading to species coexisting and interacting with novel partners both within and between trophic levels due to species-specific phenology (Rudolf 2019). These species-specific changes in phenology can lead to altered competitive (Carter & Rudolf 2019) and mutualistic relationships (Rafferty et al. 2015).

Changes in phenological relationships are of particular concern for plant-pollinator mutualisms because of plants' essential role as the foundation of terrestrial ecosystems (Behrensmeyer 1992). Over 87% of flowering plant species benefit from pollination by animal mutualists (Ollerton et al. 2011). Phenological synchrony within plant populations (Hall et al. 2018) and communities (Fisogni et al. 2022), and between plant and pollinator communities (Forrest 2015) can be highly variable. Synchronous floral displays can increase pollen dispersal and outcrossing to other individuals within and between populations (Kudo 1993; Ison et al. 2014), but can also overburden available pollinators and reduce per-flower visitation rates, resulting in pollen limitation (Thomson 2010). Asynchronous shifts in the flowering phenology and pollinator phenology can also

reduce plant and pollinator reproduction and alter population dynamics (Rafferty & Ives 2012; Ogilvie et al. 2017; de Manincor et al. 2023).

The impacts of climate change on plant-plant and plant-pollinator phenological synchrony have mainly been studied in temperate (Benadi et al. 2014), high elevation (Kudo 2014; Inouye 2020), and high latitude ecosystems (Gillespie et al. 2016). In these systems, spring temperature, photoperiod, and snowmelt are key climatic drivers of plant and pollinator phenology (Tooke & Battey 2010). However, while humid systems such as these make up a majority of landmass on Earth, dryland systems, which are defined by seasonal water deficit and represent over 40% of the world's landmass (Crawhall et al. 2012; An et al. 2021), are relatively understudied. Drylands range from dry-sub humid climates such as mediterranean and savannah environments to hyper-arid climates such as the desert of Death Valley, California (Food and Agriculture Organization of the United Nations 2023). Despite their more arid conditions, dryland ecosystems are diversity hotspots for many taxa, including plants and pollinators (Maestre et al. 2021; Minckley & Radke 2021). Plant and pollinator phenology in the dryland ecosystems of the southwestern United States can be triggered by winter temperature or precipitation, and also by summer monsoonal precipitation. The variability of phenological cues, along with the abiotic stress and the ongoing megadrought in the southwest (Mankin et al. 2021), makes phenological synchrony for plants and pollinators potentially challenging. Despite the widespread range and ecological importance of drylands, very little is known about plant-pollinator phenology and phenological synchrony in ecosystems such as the southwestern United States.

Dryland ecosystems are already relatively hot and dry, and climate change is causing further aridification (Overpeck & Udall 2020). Hotter and drier conditions threaten the physiological processes of plants and pollinators (Kazenel 2022; Yu et al. 2023), which can interact with shifting temperature and precipitation patterns to threaten plant-pollinator interactions. Before plants and pollinators can have some degree of phenological synchrony, they must for simply co-occur, which is more challenging with increasing aridification. Flowering is energetically intensive (Teixido & Valladares 2014), and floral abundance decreases with aridity (Aldridge et al. 2011). This in turn impacts pollinator populations who rely on flowers as their sole food source (Ogilvie et al. 2017). Pollinators can go into diapause if abiotic cues do not trigger phenological onset (Minckley et al. 2013), but the duration of drought can lead to permanent population declines. Studying how plants and pollinators respond to increasing aridity to maintain phenological synchrony and interaction strength is essential to understand the resilience of dryland ecosystems in a changing world.

This dissertation addresses three topics corresponding to three dissertation chapters. First, I examine how community level plant-pollinator phenological synchrony changes with aridity along an elevational gradient. Then, I use a 14-year time series to determine how phenological synchrony is changing in association with aridity for distinct plant taxa and bee guilds. Lastly, I examine how experimentally reduced plant biomass impacts phenological synchrony within and between plant populations

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Chapter 1

Plant-pollinator interaction potential varies with aridity along a dryland elevational gradient

Abstract

Climate change-driven increases in aridity may affect plant-pollinator interaction potential by altering intra-annual patterns of flowering and foraging. Using weekly data on flowering phenology and pollinator visitation spanning two consecutive years, we examined whether spatiotemporal variation in aridity predicted plant-pollinator interaction potential across a dryland ecosystem elevational gradient. At low elevations, we found that interaction partners were less likely to flower and forage in the same year and to do so with reduced synchrony under more arid conditions. High elevation sites exhibited the opposite trend, with higher likelihood of co-occurrence and synchrony associated with more arid conditions, possibly because monsoonal precipitation leading to more staggered phenology. The duration of plant and pollinator phenophases mediated these trends, with longer phenophases improving synchrony for plants but decreasing synchrony for pollinators. These results signal decreased potential for mutualistic interactions between flowering plant and pollinator communities in the most arid ecosystems, where windows of opportunity for interactions are already narrow, as aridity increases under climate change.

Introduction

Climate change is affecting species and their interactions in ecosystems across the world (McCarty 2001; Tylianakis et al. 2008; Burkle & Alarcon 2011). The linked

demographics of some mutualists, such as flowering plants and pollinators, may make them especially vulnerable to population declines if their interactions are disrupted (Kiers et al. 2010; Rafferty et al. 2015). As temperatures increase and precipitation patterns change (Bachelet et al. 2016), flowering plants and pollinators must maintain some degree of co-occurrence and phenological overlap to maintain historical interactions (Settele et al. 2016). Differential phenological shifts in flowering and foraging times can occur in response to changing climatic cues, potentially reducing interaction frequency and reproductive output (Kudo 1993; Kudo & Cooper 2019). Although plant-pollinator interactions tend to be generalized and asymmetrical (Waser et al. 1996; Ashworth et al. 2004) and can therefore be buffered from the loss of spatiotemporal overlap with some partners (Burkle et al. 2013), losses of single pollinator species from interaction networks can reduce pollination success (Brosi & Briggs 2013).

Spatiotemporal patterns in plant-pollinator interactions have mainly been studied inhumid ecosystems such as temperate (Benadi et al. 2014), high elevation (Kudo 2014; Inouye 2020), and high latitude habitats (Gillespie et al. 2016). Thus, relatively little is known about how plant-pollinator interactions vary across space and time in dryland systems (Wright et al. 2015), despite the fact that these ecosystems comprise over 40% of the global land surface (Crawhall et al. 2012). Of particular concern in dryland ecosystems is increasing aridification driven by climate change (Lian et al. 2021). Drought can increase the spatial patchiness and decrease the temporal reliability of flowering (Wright et al. 2015), cause pollinator populations to undergo extended diapause (Minckley et al. 2013), and ultimately lead to local extinctions (Fahey et al.

2018; Harrison 2020). As a result, flowering and pollinator foraging may be less likely to co-occur temporally, thereby reducing the potential for interaction. If flowering and foraging co-occur in a given season at a given site, the degree of phenological synchrony between these activities imposes an additional filter on interactions. Higher temperatures may shorten plant and pollinator phenophases (Boggs & Ross 1993; Song et al. 2022), and altered climatic patterns could change plant and pollinator phenological cues, leading to decreased phenological synchrony (Rafferty et al. 2016; CaraDonna et al. 2018). Together, the decrease in temporal co-occurrence and the further loss of phenological synchrony reduces plant-pollinator interaction potential, which can then drive changes in community composition and lead to biodiversity loss (Bellard et al. 2012).

Few studies have data of adequate temporal extent to quantify the impacts of climate change on plant and pollinator communities, especially in dryland ecosystems (but see Chapter 2). However, space-for-time substitutions along climatic gradients can provide insight into effects of long-term climatic shifts on communities (Fukami & Wardle 2005), and have been used to examine how climatic variation relates to plant-pollinator phenological synchrony (Benadi et al. 2014). Here we used an elevational gradient that allows us to assess the impacts of increasing aridity on temporal co-occurrence and phenological synchrony of flowering and pollinator foraging activity.

In this study, we collected data on flowering phenology and plant-pollinator interactions at five sites along a 2230 m elevational gradient in Southern California, USA, over two consecutive years. We determined for the first time how flower-pollinator interaction potential, quantified through temporal co-occurrence and then phenological

synchrony, varied with aridity along a dryland elevational gradient. Because physiological stress can result in decreased floral and pollinator abundance and richness (Kuppler & Kotowska 2021; Kazenel 2022), we hypothesized that plants and pollinators in a given community would be less likely to flower and forage in the same year when conditions were more arid, due to stress associated with hotter and drier conditions. We also hypothesized that phenological synchrony would decrease in more arid conditions due to shorter flowering and foraging phenophases and the greater likelihood of differential plant and pollinator phenological responses to climatic cues (Wright et al. 2015; Song et al. 2022).

Methods

<u>Study sites</u>

This study was conducted in 2021-2022 at five sites along a 2230 m elevational gradient in the Santa Rosa Mountains along the eastern edge of the Coachella Valley, CA, USA (Figure 1.1 A). The three lowest sites were located in the Boyd Deep Canyon Desert Research Center (BDCDRC), and the two upper sites in the San Bernardino National Forest (Figure 1.1 B). The lowest elevation site, site one (210 m a.s.l.), was located in a low desert wash habitat, site two (830 m a.s.l.) in a high desert habitat, site three (1300 m a.s.l.) in a high desert-pinyon pine habitat, site four (1960 m a.s.l.) in a coastal chaparral habitat, and site five (2440 m a.s.l.) in a Jeffrey pine forest habitat.

The climate along the elevational gradient is highly arid, with generally high temperatures and low precipitation (Figure 1.2). However, temperatures and precipitation vary significantly with elevation (Table 1.1). Based on local weather stations

(, accessed on 1 May 2023), site one was the hottest and driest study site. Site one and two are along the western edge of the Sonoran Desert, and receive precipitation almost entirely during the winter. Site three consists of high desert and low chaparral species and receives the bulk of its precipitation in the winter (mainly rain) with some monsoonal precipitation. Site four receives both winter (rain and snow) and monsoonal precipitation. Site five receives considerable winter snowfall as well as the highest amount of monsoonal rainfall.

Data collection

In both 2021 and 2022, we collected data weekly at each site, starting with the onset of flowering and stopping one week after all plants had ceased flowering. Mean flowering onset and cessation were positively correlated with elevation, with flowering starting in January/February at site one and ending in August at site five (Figure 1.3; Table 1.2).

Each site comprised three fixed 100 m × 10 m transects. Each transect was separated from the others by approximately 20 m. The three transects were grouped together for statistical analyses. Each week on the same day, we collected data on the community composition of plants that were flowering, floral abundances, and plant-pollinator interactions.

To document which species were flowering, we first surveyed the entire transect, noting which plants were in bloom. This initial survey enabled us to place floral abundance quadrats such that all species that were flowering on that date were represented in our flower counts. Twice per day, in the morning and afternoon, we

haphazardly placed 1×1 m^2 quadrats approximately every 10 m per transect, varying the quadrat locations to avoid double-counting the same flowers on the same date. We counted all flowers or inflorescences for each species in the quadrats, for a total of 60 m^2 surveyed per site per day. As long as all species in bloom on a given date were represented in our quadrats, we did not require that every quadrat contain at least one flower (i.e., floral abundances of zero were possible). We observed a total of 67 flowering species in 2021 and 100 species in 2022, with 61 species being observed in both years.

To collect data on plant-pollinator interactions, we surveyed each transect for 20 min four times per sampling day, for a total of 4 h of survey effort per site per day. Upon seeing an insect contacting a flower, we caught the pollinator and noted the plant species it was visiting. We identified some common visitors (*Apis mellifera*, *Xylocopa* sp., some Lepidoptera, hummingbirds) on the wing, and recorded their interactions without collecting them. We otherwise caught every pollinator we saw visiting a flower. We observed a total of 794 unique plant-pollinator interactions during 86 surveys and 344 hours of individual survey effort.

Plant and pollinator identification

We confirmed plant identification with research staff at BDCDRC.

We identified bees (Hymenoptera: Anthophila) to species (n = 672) when possible and to genus (n = 251) when not. We identified flies (Diptera) to species (n = 103), genus (n = 218), and family (n = 53). We identified wasps (Hymenoptera: Spheciformes) to species (n = 49), genus (n = 22) and family (n = 5). Specimens not identified to species

were enumerated. We observed 73 butterflies and moths (Lepidoptera) and identified

them to species (n = 54) or morphospecies (n = 7). Voucher specimens were deposited in

the Entomology Research Museum at the University of California, Riverside.

Quantifying interaction potential

For plants and pollinators to be observed interacting in our surveys, flowers and

foraging pollinators must be present at the same time. Thus, flowering and foraging

within the same year acts as a first filter on interaction potential, with the magnitude of

phenological overlap (synchrony) in flowering and foraging acting as a second filter. Not

all species bloomed in both years (61/106 species), and there was significant turnover in

pollinator community composition between years (305 of 401 taxa were present only in

2021 or 2022). To assess temporal co-occurrence, we used a binomial metric for plants

and pollinators that were observed to interact in a given site in either year (i.e., potential

partners). Instances where potential partners were both flowering/foraging at the same

site in the same year were considered to co-occur (1). Instances where one or both

partners were not flowering/foraging in a given site and year were considered complete

phenological mismatches (0).

To estimate phenological synchrony between temporally co-occurring plant-

pollinator species pairs, we imputed daily-resolution phenological distributions for each

species × site × year combination using von Mises kernel density from the densityFit

function in the R package overlap (Ridout & Linkie 2009). We selected distribution

sensitivity (bandwidth) using the vm.kde function in the R package Directional (Tsagris

et al. 2023). For plant species, we imputed distributions using data from the floral

abundance surveys. To determine pollinator phenological distributions, we used the

number of specimens collected (or number of individuals counted for species identified

on the wing) during the weekly plant-pollinator surveys, summing the number of times a

species was caught during the four surveys for each date. Finally, we scaled phenological

distributions from 0-1, such that the day of year of peak abundance for a given species

equaled 1.

To calculate phenological synchrony, we quantified the proportion of overlap

between the imputed plant and pollinator phenological distributions. We performed

pairwise comparisons of the distributions of all pollinator and plant species known to

interact, modifying methodology from Carter et al. (2018), Stemkovski et al. (2020), and

Fisogni et al. (2022). For each species pair, we quantified the shared area under the

phenological distributions of the two species. We then compared the shared area to the

phenological distributions of each species' individual distribution. This yielded, for each

bee and plant species separately, the proportion of its distribution shared with its

interaction partner, with 0 indicated no phenological overlap and 1 indicating complete

phenological overlap.

<u>Quantifying aridity</u>

To determine how temporal co-occurrence and phenological synchrony varied

with aridity along the elevational gradient, we used the standardized precipitation

evapotranspiration index (SPEI; Beguería & Vicente-Serrano 2017). SPEI incorporates

temperature and precipitation into one metric, with negative values being more arid, and

positive values being less arid. For the lower three sites we used temperature and

precipitation data from the BDCDRC weather stations located within 30-1200 m of each site. For sites four and five, we used monthly averages extracted from 800 m grid cells from the parameter-elevation regressions on independent slopes model (PRISM) climate group database (Oregon State University, https://prism.oregonstate.edu, data created 2023).

For analyses related to temporal co-occurrence, we averaged the 12-month lag of SPEI values of the plants and pollinators that flowered or foraged in a given site and year, thereby encompassing the range of conditions that triggered the activities enabling interaction for each local community as a whole.

As opposed to the site averaging for co-occurrence analyses, we calculated SPEI for the 12 months prior to phenological onset for each plant and pollinator species included in phenological synchrony analyses (i.e., onset of flowering or foraging). This produced a unique value for each plant and pollinator species that flowered/foraged in different months and years. We combined data from 2021 and 2022 to provide greater variation in aridity. Because we set the SPEI with a 12-month lag, there is little to no overlap in the climate data used to quantify aridity in 2021 and 2022.

Statistical modeling

To determine whether temporal co-occurrence varied with aridity along the elevational gradient, we used a generalized linear model (GLM) with a binomial error distribution and logit-link with temporal co-occurrence (0,1) as the response variable, and SPEI, elevation, and their interaction as predictors.

To determine whether phenological synchrony from the plant or pollinator perspectives varied with aridity along the elevational gradient, we fitted GLMs with an ordered beta error distribution using phenological synchrony (0-1) as the response variable, and SPEI, elevation and their interaction as predictors. For analyses with phenological synchrony as the response, we fitted separate models for plant and pollinator perspectives. Separating plant and pollinator perspectives allowed us to better incorporate the variable duration of phenophases. For example, a synchrony value of 1 for a species that was phenologically active only for two weeks is more likely than a synchrony value of 1 for a species that was phenologically active for four weeks.

Models were fitted using the R package glmmTMB (Brooks et al. 2017). All analyses were conducted in R 4.3.0 (R Core Team 2013).

Results

Plant-pollinator partners had higher probability of temporal co-occurrence when conditions were less arid at all sites except the highest elevation site, where the probability of temporal co-occurrence increased when conditions were more arid (Figure 1.4 A; Table 1.3). For the four lower elevation sites, the probability of temporal co-occurrence was greater than 75% at the lowest levels of aridity, while the probability declined to 25% for partners at the lowest elevation site under the most arid conditions.

Plant-pollinator phenological synchrony was higher from both the plant perspective (Figure 1.4 B, Table 1.3) and pollinator perspective (Figure 1.4 C, Table 1.3) in less arid conditions at all sites, except the highest elevation site.

The duration of flowering and pollinator foraging periods decreased in more arid conditions, with the most negative slope occurring at lowest elevation (Figure 1.4 A-B, Table 1.4 A-B). Longer periods of flowering increased plant phenological synchrony, with the strongest trend occurring at lower elevations (Figure 2C, Table 1.4 C). Longer pollinator foraging periods decreased pollinator phenological synchrony, with no differences among sites (Figure 2 D, Table 1.4 D).

Discussion

We found that plant-pollinator interaction potential varied with aridity and depended on elevation. The lowest elevation sites had both the lowest degree of phenological synchrony in highly arid conditions and the highest degree of synchrony in the least arid conditions, whereas synchrony increased with aridity at the highest elevation site. The duration of flowering and pollinator foraging decreased in more arid conditions, but whereas greater duration of flowering was associated with greater phenological synchrony with pollinators, the opposite was true for pollinator foraging duration. This is the first study to examine the impact of aridity on plant-pollinator temporal co-occurrence and phenological synchrony along a dryland elevational gradient and provides key insights into the future of plant-pollinator interaction potential in an increasingly arid world.

Increasing aridity can have a number of physiological and ecological effects on plants and pollinators that could result in decreased interaction potential. Because flowering is energetically intensive (Teixido & Valladares 2014) and is a major source of water loss during physiologically stressful conditions (Bourbia et al. 2020), plants

typically respond to highly arid conditions by either not producing flowers at all or producing fewer flowers and flowering for shorter durations (Phillips et al. 2018; Kuppler & Kotowska 2021). This could directly impact co-occurrence in our study as it is not independent in that pollinators were caught on plants, necessitating floral presence to identify foraging pollinators. Our results suggest that plants in dryland ecosystems conserve resources and have shorter flowering periods under more arid conditions. Although shorter flowering periods were associated with reduced phenological synchrony of plants with pollinators, shorter foraging periods were associated with greater synchrony of pollinators with flowers. Thus, from the plant perspective, higher aridity may impose a trade-off between the benefits of energy conservation via reduced flowering duration and the costs of reduced synchrony with pollinators. From the pollinator perspective, higher aridity may shorten foraging duration and increase the importance of synchronously emerging with floral onset.

In this study, plant and pollinator communities that had lower probability of temporal co-occurrence also had a lower degree of phenologically synchronous. This is in contrast to a recent study that showed temporal co-occurrence to be less sensitive than phenological synchrony to aridity (Chapter 2). Abiotic conditions in this study were more arid than in Chapter 2 suggesting that the degree of aridity was severe enough in the dryland elevational gradient studied herein to impact both temporal co-occurrence and synchrony of interacting partners. Additionally, Chapter 2 relied on presence data, whereas this study used interaction data, which suggests species presence does not necessarily translate into interactions between plants and pollinators. Pollinators such as

bees (Forrest et al. 2019; Shi et al. 2023), and especially floral specialists (Minckley et al. 2013), are often able to go into diapause and skip seasons or years when highly arid conditions such as drought do not trigger emergence. Alternatively, generalists often adaptively forage on whichever floral resources are most abundant (Minckley et al. 2013). The intensity of the aridity in this study could prevent the majority of pollinators within a population from becoming phenologically active and instead maintaining a state of diapause, which could then lead to population declines in these drylands, which contain one of the most diverse communities of bees globally (Minckley & Radke 2021). Additionally, it is important to note that, while outside of the scope of this study, pollinator's mobility could play an important role in shifting pollinators to higher elevation habitats that are less arid.

Our finding that the highest elevation plant and pollinator communities had higher interaction potential in more arid conditions suggests that species in those communities may respond differently to drought than communities at the lower elevations. At the highest elevations, low aridity in parts of the year can be moderated by exceptionally wet monsoon seasons, as was the case in 2022. Staggered precipitation events could lead to reduced synchrony in flowering and foraging if the phenologies of some species are triggered by earlier precipitation events and other species are triggered by later precipitation events. Large precipitation events are becoming less common in the monsoonal southwest (Petrie et al. 2014), and therefore, interacting species may not respond the same way to future precipitation events as the sensitivity of phenological

cues differs between taxa. Phenological cues are becoming less distinct, potentially altering plant-pollinator phenological synchrony.

Conclusions

Together, our findings indicate that plants and pollinators in the dryland ecosystem studied here have reduced interaction potential in more arid conditions at lower elevations. Given the current mega-drought and projections of intensifying aridification in this region (Mankin et al. 2021; Williams et al. 2022), these results suggest that the plant and pollinator communities in the most arid habitats are likely to experience the greatest declines in interaction potential, potentially signaling the deterioration of plant-pollinator phenological synchrony at higher elevations under future climates.

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Tables, Images, & Figures

Table 1.1: Average (+/- standard deviation) temperature, precipitation, and aridity (standardized precipitation evapotranspiration index; SPEI) at each site during the time period included in the study (January 2021 – September 2022).

Site	Elevation (m a.s.l.)	Temperature C (+/- SD)	Precipitation mm (+/- SD)	SPEI (+/- SD)
1	210	26.1 (+/- 6.9)	2.3 (+/- 5.5)	-0.334 (+/- 1.019)
2	830	22.5 (+/- 7.0)	6.2 (+/- 10.5)	-0.289 (+/- 0.850)
3	1300	21.8 (+/- 7.3)	10.7 (+/- 18.3)	-0.421 (+/- 0.883)
4	1960	12.4 (+/- 6.7)	26.3 (+/- 45.8)	-0.393 (+/- 0.915)
5	2440	9.4 (+/- 6.5)	36.1 (+/- 62.4)	-0.010 (+/- 0.910)

Table 1.2: Model results for phenological onset and senescence for plants and pollinators predicted by elevation. Model estimates, standard errors, z values, and p values are given for each predictor.

Taxa	Year	Phenological trait	Estimate	Std error	Z value	P value
Plants	2021	Onset	0.043	0.003	14.87	<0.001
Plants	2021	Senescence	0.042	0.004	11.17	<0.001
Plants	2022	Onset	0.051	0.003	20.182	<0.001
Plants	2022	Senescence	0.052	0.003	19.16	<0.001
Pollinators	2021	Onset	0.045	0.002	20.71	<0.001
Pollinators	2021	Senescence	0.046	0.002	18.69	<0.001
Pollinators	2022	Onset	0.047	0.002	23.61	<0.001
Pollinators	2022	Senescence	0.049	0.002	23.29	<0.001

Table 1.3: Model results for A) plant-pollinator temporal co-occurrence predicted by aridity (standardized precipitation evapotranspiration index; SPEI), elevation, and their interaction, B) plant phenological synchrony predicted by aridity (standardized precipitation evapotranspiration index; SPEI), elevation, and their interaction, and C) pollinator phenological synchrony predicted by aridity (standardized precipitation evapotranspiration index; SPEI), elevation, and their interaction. Model estimates, standard errors, z values, and p values are given for each predictor.

A) Plant-pollinator temporal co-occurrence			
Predictor	Estimate	Std error	Z value	P value
SPEI	0.557	0.115	4.851	<0.001
Elevation	-0.79	0.188	-4.208	<0.001
SPEI * Elevation	-0.629	0.125	-5.03	<0.001
B) Phenological synchrony: Plants			
Predictor	Estimate	Std error	Z value	P value
SPEI	2.8731	0.5647	5.088	<0.001
Elevation	1.1167	0.3278	3.406	0.001
SPEI * Elevation	-3.2437	0.659	-4.922	<0.001
C) Phenological synchrony: Pollinators			
Predictor	Estimate	Std error	Z value	P value
SPEI	2.366	0.635	3.724	<0.001
Elevation	1.165	0.357	3.261	0.001
SPEI * Elevation	-2.86	0.734	-3.897	<0.001

Table 1.4: Model results for A) plant duration predicted by aridity (standardized precipitation evapotranspiration index; SPEI), elevation, and their interaction, B) Pollinator foraging duration predicted by the aridity, elevation, and their interaction, and C) plant phenological synchrony predicted by aridity, plant duration, and their interaction, and D) pollinator phenological synchrony predicted by aridity, pollinator foraging duration, and their interaction. Model estimates, standard errors, z values, and p values are given for each predictor.

A) Plant duration ~ aridity * elevation				
Predictor	Estimate	Std error	Z value	P value
SPEI	39.671	10.901	3.639	<0.001
Elevation	9.786	6.338	1.544	0.123
SPEI * Elevation	-32.635	12.717	-2.566	0.001
B) Pollinator duration ~ aridity * elevation				
Predictor	Estimate	Std error	Z value	P value
SPEI	59.85	12.82	4.669	<0.001
Elevation	32.82	7.316	4.486	<0.001
SPEI * Elevation	-61.466	14.84	-4.142	<0.001
C) Plant phenological synchrony ~ duration * elevation				
Predictor	Estimate	Statistic	Degrees of freedom	P value
Duration	2.431	0.407	5.967	<0.001
Elevation	0.311	0.264	1.179	0.238
Duration * Elevation	-1.411	0.57	-2.478	0.001
D) Pollinator phenological synchrony ~ duration * elevation				
Predictor	Estimate	Std error	Z value	P value
Duration	-0.871	0.397	-2.194	0.002
Elevation	-0.136	0.163	-0.836	0.403
Duration * Elevation	-0.106	0.5	-0.211	0.083

Figure 1.1: This study was located in Riverside County, California, US in 2021 and 2022. Survey sites were located in Boyd Deep Canyon Desert Research Center (sites 1-3), and the San Bernardino National Forest (sites 4-5). Elevations range from 201 m a.s.l. to 2440 m a.s.l.

Figure 1.2: A) Trends in aridity (standardized precipitation evapotranspiration index; SPEI) at each site from 1990 to 2023. B) Linear regression results for aridity at each site from 1990 to 2023. C) Linear regression results for aridity at each site from 2016 to 2023.

Figure 1.3: Trends in phenological onset (green) and senescence (red) for plants (A) and pollinators (B) in 2021 and 2022 in relation to their site's elevation. Dates of onset and senescence significantly increase with elevation for plants and pollinators in both years.

Figure 1.4: Model results for A) temporal co-occurrence, B) plant phenological synchrony, and C) pollinator phenological synchrony predicted by aridity (standardized precipitation evapotranspiration index; SPEI), elevation, and their interaction. Each site is represented by its elevation. Significance for individual predictors and their interaction are indicated by asterisks in the axis and legend.

Figure 1.5: Model results for A) floral duration, and B) pollinator foraging duration predicted by aridity (standardized precipitation evapotranspiration index; SPEI), elevation, and their interaction. Model results for C) plant phenological synchrony predicted by floral duration, elevation, and their interaction, and for D) pollinator phenological synchrony predicted by pollinator foraging duration, elevation, and their interaction. Each site is represented by its elevation. Significance for individual predictors and their interaction are indicated by asterisks in the axis and legend.

Chapter 2

Synchrony of flowering and bee flight periods over 14 years is reduced with increasing aridity

Abstract

Climate change can disrupt species interactions by offsetting the phenologies of interacting species, including plants and pollinators. Although evidence for phenological mismatches is scant, most studies lack long-term data on entire phenological distributions and focus on humid systems. Here, we used 14 years of data to examine how synchrony of flowering and bee flight periods have shifted with climate for three plant taxa and seven bee guilds in three dryland ecosystems that have become more arid and are predicted to continue to become more arid. Phenological synchrony decreased under more-arid conditions for six of the seven bee guilds and two of the three plant taxa, and the degree to which synchrony was maintained depended on interaction breadth. Our findings indicate synchrony may decrease with increasing aridity for most interacting bee guilds and plant taxa, suggesting future aridification of drylands could reduce the ecosystem service of bee pollination.

Introduction

Climate change can alter the abiotic cues that shape phenology, the timing of life history events (Chmura et al. 2019). When species respond differently to climatic cues, climate change can disrupt their interspecific interactions by decreasing phenological synchrony, the degree of temporal overlap between interacting species at particular phenophases, or life history events (Encinas-Viso et al. 2012). Mutualisms, such as those

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between flowering plants and pollinators, may be especially vulnerable to phenological asynchrony because they have short phenological durations. Indeed, simulations suggest that phenological shifts can disorganize plant-pollinator mutualisms (Memmott et al. 2007). For plants, shifts in flowering phenology can reduce pollinator visitation and effectiveness, decreasing fruit and seed set (Rafferty & Ives 2012; Kudo & Cooper 2019). As more than 87% of flowering plant species rely on animals for pollen transfer, pollinators maintain plant diversity and ecosystem functioning (Ashman et al. 2004; Ollerton et al. 2011; Wei et al. 2021). For pollinators, asynchrony with flowers can reduce food supply, causing them to forage on less nutritious floral resources, or to travel further to collect floral resources (Westphal et al. 2006). For bee pollinators, low quantity and/or quality of pollen can disrupt larval development (Wilson Rankin et al. 2020). Indeed, reduced floral abundances and shifts in flowering times have been associated with declines in bee populations (Ogilvie & Forrest 2017; Ogilvie et al. 2017).

Whether and in what systems climate change will generate plant-pollinator phenological mismatches remains an open question. On one hand, natural selection is expected to maintain phenological overlap between plants and pollinators (Forrest & Miller-Rushing 2010; Rafferty et al. 2015). However, if partners rely on different environmental cues, as occurs in some systems (Rafferty et al. 2016; CaraDonna et al. 2018), or differ in their sensitivities to those cues (Forrest & Thomson 2011), then climate change could offset matched phenologies, decreasing phenological overlap of specific plant-pollinator pairs. Additionally, asynchrony could occur if the rate of climate change outpaces adaptive responses (Quintero & Wiens 2013), although interacting

partners may maintain phenological synchrony in response to environmental change via phenotypic plasticity (Iler et al. 2017). Observational studies examining plant and pollinator phenological responses to environmental cues have generally found little evidence that changing climatic conditions will result in phenological mismatches due to differing responses to climatic shifts (Forrest 2015; Renner & Zohner 2018). Nevertheless, climatic change is predicted to reduce plant-pollinator phenological synchrony in some habitats such as mediterranean and alpine systems (Olliff-Yang & Mesler 2018; Kudo & Cooper 2019).

Plants and pollinators fall on a spectrum of evolutionary specialization that may shape the likelihood of phenological asynchrony with partners as the climate shifts. While specialized mutualists are predicted to be better synchronized with their partners, generalized mutualists may be buffered from phenological mismatches by interacting with many partners with varied phenologies (Rafferty et al. 2015). Therefore, for generalized pollinators and plants, mismatches may not be detrimental if overlap with functionally redundant partners is maintained (Burkle & Alarcon 2011; Bartomeus et al. 2013). However, experimental manipulation of pollinator community composition phenology likely reduced plant reproduction (Brosi & Briggs 2013), suggesting that subtle changes in phenological synchrony can alter selection (Gienapp et al. 2014). Furthermore, plant-pollinator interactions are often asymmetrical, with most specialist pollinators relying on generalist plants, and a minority of reciprocally specialized interactions (Ashworth et al. 2004). In drylands, where bee guilds often specialize on super-generalized plants (Cane et al. 2005), loss of phenological synchrony could be

detrimental to a specialized pollinator species but come at little cost to the plant. We can improve our understanding of the impacts of climate change on phenological synchrony when we consider that plants and their pollinator guilds may be under different constraints related to differences in interaction breadth (the richness of partners a species interacts with), which may shape phenological responses of individual species and therefore synchrony with other species.

In addition, by using phenological distributions of populations, which capture the abundances of individuals at a given phenophase, instead of discrete phenological summaries (e.g., onset, peak, cessation) to quantify the degree of overlap between interacting partners, we can better understand plant-pollinator phenological synchrony. Few studies have examined phenological synchrony from both the plant and pollinator perspectives using phenological distributions; most instead analyze synchrony using difference-based metrics (e.g., difference between phenological onset/peak/senescence [Rafferty et al. 2013; Maglianesi et al. 2020]; or compare the rates of phenological response between species, measured over time or per unit change in climatic variables, to infer changes in synchrony (Bartomeus et al. 2011; McKinney et al. 2012). Using difference-based metrics can be misleading, especially when multiple peaks and phenophases occur in the same year, as in bimodal flowering in spring and monsoonal seasons in dryland ecosystems. By capturing the density of individuals in a given phenophase, phenological distributions can more accurately quantify phenological synchrony. A recent study found that, among species, phenological distributions of flowering have decreased in synchrony in the southwestern United States (Fisogni et al.

2022), but no prior studies have analyzed plant-pollinator synchrony using distribution-based approaches.

Most previous studies of plant and pollinator phenological responses have been situated in ecosystems where changes in snowmelt timing and spring temperatures are associated with relatively unidirectional shifts in plant and pollinator phenophases, e.g., in humid temperate (Bartomeus et al. 2011), high elevation (Inouye 2020), and high latitude systems (Gillespie et al. 2016). In dryland environments, however, patchy, inconsistent flowering through space and time can be common (Wright et al. 2015). This is seen in locations where monsoonal precipitation patterns, which are changing in distribution and intensity (Petrie et al. 2014; Demaria et al. 2019), dictate phenology (Forzieri et al. 2011). Changing climatic cues can cause plants to shift their flowering phenologies in multiple directions over small spatial scales (Rafferty et al. 2020), potentially leading plants and pollinators in dryland environments to be more susceptible to phenological mismatches. Understanding how phenological synchrony is changing in dryland environments, where native bee diversity is often highest (Minckley & Radke 2021), is especially important given the lack of research and the stochastic nature of phenological cues.

In this study, we used variation in aridity over a 14-year time series to quantify how phenological overlap between three common plant taxa and their bee guilds has changed in association with climatic change in three dryland ecosystems in central New Mexico, United States. We hypothesized that plant-bee phenological synchrony, both between species pairs and between individual species and the communities of taxa with

which they interact, would be reduced under more-arid conditions as taxa reach the limits of phenological change (Iler et al. 2013). We further hypothesized that the incidences of complete phenological mismatches (i.e., no temporal overlap) would increase with aridity.

Methods

Study sites and focal plant taxa

All data were collected at the Sevilleta National Wildlife Refuge (SNWR), located on the northern edge of the Chihuahuan Desert in central New Mexico, United States. The SNWR includes several ecosystem types, including Chihuahuan desert grassland, plains grassland, and creosote shrubland. Total annual precipitation is ~250 mm, with ~60% occurring during the summer monsoon from July through early September (Notaro et al. 2010). The SNWR has become more arid on average over the past 120 years and especially during the interval between 1989 and 2015 (Rudgers et al. 2018). Data on bee and plant phenology were collected within three ecosystem types that together represent ~60 million ha of the southwestern United States: Chihuahuan Desert shrubland, which is dominated by creosote bush *Larrea tridentata* (Moc. & Ses.) Cav. (Zygophyllaceae), Chihuahuan Desert grassland, which is dominated by black grama grass (*Bouteloua eriopoda* (Torr.) Torr. [Poaceae]), and Plains grassland, which is dominated by blue grama grass (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths [Poaceae]). The two Chihuahuan Desert sites were separated by ~2 km; the Plains grassland site was ~10 km from the Chihuahuan Desert sites.

We selected three focal plant taxa for our analyses: plants in the family Cactaceae, *Larrea tridentata* (Zygophyllaceae), and plants in the genus *Sphaeralcea* (Malvaceae). The flowers of each of these taxa are visited by large guilds of bees, including species that are known to specialize on each plant taxon (Hurd & Linsley 1975; Cane et al. 2005; Pendleton et al. 2008). At the SNWR, there are 19 species of Cactaceae. Cactus are extremely drought tolerant with succulent stems and often large showy flowers. Species typically flower only in the spring, are uniquely native to the Western Hemisphere, and are particularly abundant in the American Southwest. At least 29 native bee species, spanning 4 families, have been confirmed visiting cactus flowers at the SNWR.

Larrea tridentata is a resinous flowering shrub that dominates floras of most warm desert basins of the USA and adjacent Mexico (T. J. Mabry et al. 1977; Raymond M. Turner et al. 1995). *Larrea tridentata* is visited by a taxonomically diverse assemblage of >100 species of native bees (Hurd & Linsley 1975; Minckley et al. 1999), making it one of the most species-rich pollinator guilds known (Wcislo & Cane 1996). *Larrea tridentata* is generalized in its interactions with pollinators, attracting many polylectic and oligolectic bees; of the latter, 21 species are narrowly oligolectic (sensu Cane & Sipes, 2006). Its floral phenology is highly sensitive to precipitation, with 12 mm of rainfall sufficient to induce flowering (Bowers & Dimmitt 1994). At the SNWR, *L. tridentata* floral abundance typically peaks in the spring and monsoon seasons, and 54 bee species are documented visitors (Wright and Bettinelli, unpublished).

There are six *Sphaeralcea* species present at SNWR, including annuals and herbaceous or semi-woody perennials. The genus is present in most arid environments in

the southwestern US. *Sphaeralcea* bloom in the spring and monsoon seasons hosting a diverse bee guild at the SNWR, with 46 bee species documented .

Data collection

Bee and plant data were collected within three sites, each representing one of the three focal ecosystem types, along five 200 m transects per site. Bee abundance was determined monthly using passive funnel traps from 2002-2015. Traps were opened each March as close as possible to the first day of spring, and left open for 14 days, after which the bee specimens were collected. The traps were then closed for 14 days. This two-week cycle was repeated through October. A detailed description of the traps and methodology can be found in Kazenel et al. (2020).

Bees were identified to species by co-authors K. W. Wright and T. L. Griswold. Voucher specimens were deposited at the University of New Mexico's Museum of Southwestern Biology and the USDA-ARS Pollinating Insects Research Unit's U.S. National Pollinating Insects Collection. Information related to these specimens is available via the Symbiota Collections of Arthropods Network (https://scan-bugs.org). A total of 197273 bee specimens were used in this study.

Data on the flowering phenologies of angiosperms were collected once per month from March through October along four of the five 200 m transects at each site. The phenological condition of the first 10 individuals of each species encountered along the transect was recorded. For Cactaceae and *Sphaeralcea* taxa, the number of individual plants in bloom for each species was counted; these species were then pooled by taxonomic group for analyses. This method does not account for differences in floral

abundances between individual plants; plants with any number of flowers were considered in flower. For our analyses, we calculated the proportion of plants in flower for each taxon per site per month.

<u>Literature review of bee visitors to focal plant taxa</u>

We performed a literature review to determine which bee species collected in traps were known visitors of the three focal plant taxa in our study. This effort was necessary because the Sevilleta bee community is hyperdiverse (341 species), and it is not feasible to document all floral resources exploited by each bee species via field observations. To conduct the standardized literature review, we searched Web of Science during May and June of 2020 using the terms "*plant taxon* AND (bee OR pollin*) AND (southwest* OR New Mexico OR Arizona OR Texas OR California)" in all fields for years 1900-2020. We also searched using the terms "*Bee genus name* AND (diet breadth OR diet OR breadth OR special* OR oligolec* OR polylec*) AND (pollinat* OR pollen) AND (southwest* OR New Mexico OR Arizona OR Texas OR California)". We applied these terms for each focal plant taxon and bee genus present at the SNWR. From the 95 papers that matched our terms (N = 46 for Cactcaeae, 11 for *L. tridentata*, 4 for *Sphaeralcea*, 34 for all bee genera), we searched for documented interactions between our focal plant taxa and bee species known to be present at our study site.

In addition to the literature review, we used an unpublished database of observed interactions from the SWNR (Wright and Bettinelli, unpublished). We limited analysis of phenological overlap to species pairs with documented interactions. The literature search and unpublished datavase revealed that Cactaceae were visited by a total of 25 bee

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species, *L. tridentata* was visited by 46 bee species, and *Sphaeralcea* were visited by 52 bee species.

We differentiated between specialized and generalized bee guilds based on the evolutionary specificity of their interactions. Specialized bees visited plants in a single taxon (which varied from a single species to a single family) and did not visit plant taxa outside of the three groups considered in this study. Generalist bees were considered species that visited more than one of our focal plant taxa, and may have also visited plant taxa outside of the scope of this study. This produced four guilds of generalists: three species that visited Cactaceae and *L. tridentata* (hereafter denoted C+L), two species that visited Cactaceae and *Sphaeralcea* (hereafter denoted C+S), four species that visited *L. tridentata* and *Sphaeralcea* (hereafter denoted L+S), and eight species that visited all three focal taxa (hereafter denoted C+L+S; Table 2.1). Specialist bee guilds consisted of two Cactaceae specialist species, two *L. tridentata* specialist species, and five *Sphaeralcea* specialist species.

Prior to analyses, we applied sample size thresholds at the species level for bees, including data on only those bee species for which at least three individuals were collected at any given site, and that were present in at least three of the 14 years in our time series. These thresholds removed a minority of bee visitors to Cactaceae taxa (53% remaining) and *Sphaeralcea* taxa (52% remaining), and a majority of bee visitors to *L. tridentata* (34% remaining).

We quantified aridity to explore the correlation between climate and plant and pollinator phenological synchrony. Because the climate in the northern Chihuahuan Desert has become more arid over the past 120 years (Rudgers et al. 2018) and can be highly variable between years (Lasché et al. 2023), our time series captures a wide range of aridity to gain insight into future impacts of climate change. We quantified aridity by calculating the Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al. 2014) for one, two, three, and six month sliding windows of time preceding each phenophase of interest (e.g., flowering onset or bee flight onset). We also calculated SPEI for the duration of each phenophase, yielding five SPEI metrics (four that encompass conditions at different periods of time prior to and relative to the phenophase and one that encompasses conditions during the phenophase) that we evaluated as separate predictors in models. SPEI values were calculated using daily climate data from two on-site meteorological stations (plains grassland: 34.3350, -106.6313; Chihuahuan Desert shrubland and Chihuahuan Desert grassland: 34.3351, -106.7287). The two relatively close sites (Chihuahuan Desert shrubland and Chihuahuan Desert grassland) share data from a single meteorological station. We calculated SPEI in two ways for each species × site × year using the package SPEI (Santiago, and Vicente-Serrano 2017). SPEI prior to phenophase captures how climate may serve as a phenological cue, while SPEI during the phenophase predicts how aridity impacts proportional abundances throughout the seasons of activity. SPEI was calculated using the SPEI package (Beguería &

Vicente-Serrano 2017), and all analyses were conducted in R version 4.1.2 (R Core Team 2020).

<u>Plant-bee phenological synchrony</u>

To calculate phenological synchrony, we quantified the degree of overlap between bee and plant phenological distributions. We imputed daily-resolution phenological distributions for each bee and plant species × site × year combination using von Mises kernel density from the 'densityFit' function (bandwidth = 20; Ridout & Linkie 2009). We selected a bandwidth of 20 because the imputed data closely matched the raw data without overemphasizing the gaps between monthly data points. von Mises kernels capture the circular distribution of phenological data, accounting for the fact that the final day of one year and the first day of the following year are only one day apart, rather than maximally distant as represented on a linear scale (Staggemeier et al. 2020). Because the methods used to collect raw abundance data differed for bees and plants, we scaled annual bee species abundance and plant species proportional abundance from 0-1 to facilitate comparisons (Figure 2.1). Although this scaling means that our phenological distributions do not reflect absolute differences in abundance between bees and plants at a given phenophase, any bias it introduces should be consistent across taxa, particularly because our prior thresholds removed bee species that were rare or infrequently detected. We then did pairwise comparisons of the distributions of all bee and plant species known to interact, modifying methodology from Carter et al. (2018), Stemkovski et al. (2020), and Fisogni et al. (2022). For each species pair at each site and year, we quantified the shared area under the phenological distributions of the two species. We then compared

the shared area to the total area under the distribution of each individual species (Figure 2.1). This yielded, for each bee-plant pair at each site and year, the proportion of the bee and plant distributions that each species shared with the other (i.e., from each species pair, two synchrony values were calculated; hereafter this method is denoted 'pairwise phenological synchrony method').

For each plant taxon and bee guild (Three specialist bee guilds and four generalist bee guilds), we fit a set of candidate models to determine if pairwise phenological synchrony was predicted by aridity. We used generalized linear models with ordered beta error distributions in the glmmTMB package (Brooks et al. 2017; Kubinec 2022). Beta distribution models are most appropriate for proportional response data such as our phenological synchrony metric (Douma & Weedon 2019). For each of our five candidate models, pairwise phenological synchrony (proportion of bee-plant overlap) was the response, and one of the five SPEI metrics was the predictor (fixed effect), with year and site as random effects. All models had normal residuals, dispersion, and outliers according to the simulateResiduals function in the DHARMa package (Hartig & Lohse 2022). We checked all models for autocorrelation with the check_autocorrelation function in the performance package (Lüdecke et al. 2021), and one model (C+L+S generalists) still had significant autocorrelation after adding an AR1 covariance structure.

Synchrony for pairs of taxa vs. communities

To better assess how phenological synchrony has changed for taxa with different interaction breadths, we created cumulative phenological distributions for entire bee guilds and plant taxa. To do so, we pooled the phenological distributions of all species

within a taxonomic group such that, when multiple taxa were detected on a single date, data on the species with the highest proportional abundance on that date was selected to create the distribution. This produced one composite phenological distribution for each bee guild or plant taxon per site per year (hereafter denoted 'community-level phenological synchrony method'). We included rare bees (that did not reach the sample size thresholds applied to the data used in the pairwise phenological synchrony method) in these community-level phenological distributions to better represent the entire bee community that our focal plant taxa interacted with. We fit models to determine whether phenological synchrony was predicted by aridity and phenological synchrony method (pairwise phenological synchrony method vs. community-level phenological synchrony method). We constructed candidate models with synchrony as the response, and one of the five SPEI metrics, the phenological synchrony method, and the interaction between the two as predictors. We included year and site as random effects and used generalized linear models with ordered beta error distributions in the package glmmTMB. All models had normal residuals, dispersion, and outliers. Three models had significant autocorrelation (C+L generalists, *L. tridentata*, and *Sphaeralcea* plants) after applying AR1 covariance structures.

Co-occurrence and phenological overlap

Plants and bees must co-occur in time and space to interact. Complete phenological mismatches (synchrony = 0), where both taxa co-occurred in a given site and year but did not overlap phenologically, were rare (0% of all synchrony values for plants and 2% of all synchrony values for bees using the pairwise phenological

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synchrony method, Table 2.). In contrast, there were many instances in which one or both

taxa were absent at a given site and in a given year (42-89%). We term these taxonomic

pairs transiently non-co-occurring. Transient non-co-occurrence and complete

phenological mismatches are functionally the same, as bees and plants do not have the

potential to interact. To determine how the proportion of co-occurring and phenologically

overlapping taxonomic pairs changed as a function of aridity, we divided the number of

co-occurring and phenologically overlapping taxonomic pairs by the maximum number

of potentially interacting taxonomic pairs per focal taxon per year. This metric provides

information that the synchrony models do not capture. We built candidate models with

the proportion of co-occurring and phenologically overlapping species pairs as the

response and with one of four SPEI metrics (SPEI prior to flight period or flowering) as

the predictor, with year and site as random effects. All models had normal residuals,

dispersion, and outliers. Three models had significant autocorrelation (*Sphaeralcea*

specialists, C+S generalists, and L+S generalists) after applying AR1 covariance

structures.

<u>Model selection and fitting</u>

We compared candidate models using the AICtab function from the lmtest

package (Hothorn et al. 2022) to select the best-fitting models for each focal taxon for our

three main analyses: plant-bee phenological synchrony; synchrony for pairs of species vs.

communities; and co-occurrence and phenological overlap (Table 2.3). In total, we

reduced our candidate model set down to 30 best-fitting models (one for each bee

guild/plant taxa and analysis).

Results

<u>Plant-bee phenological synchrony</u>

Phenological synchrony declined with greater aridity for all plant taxa and bee guilds for which aridity was a significant predictor of synchrony (all three plant taxa and five of the six bee guilds), with the exception of Cactaceae and bees that specialize on Cactaceae (Figure 2.2 A-C; Table 2.4 A). For four of the six bee guilds for which aridity was a significant predictor of phenological synchrony with flowers, the degree of synchrony was best predicted by SPEI during their flight periods, rather than prior to emergence (Figure 2.2 A-B). In contrast, the synchrony of plant taxa flowering with their bee guild flight times was most sensitive to aridity prior to flowering, with Cactaceae synchrony predicted by aridity three months prior to flowering onset, *L. tridentata* synchrony predicted by aridity two months prior to flowering onset, and *Sphaeralcea* synchrony predicted by aridity six months prior to flowering onset (Figure 2.2 C). Cactaceae taxa had significantly reduced synchrony with bees when conditions were less-arid prior to flowering, while *L. tridentata* and *Sphaeralcea* taxa had significantly greater synchrony with bees when conditions were less-arid preceding flowering.

<u>Synchrony for pairs of taxa vs. communities</u>

All bee guilds, with the exception of *L. tridentata* specialists, and all plant taxa had significantly greater phenological synchrony when considering their community-level synchrony compared to pairwise taxonomic synchrony (Figure 2.3, Table 2.4 B). Pairwise phenological synchrony and community-level synchrony changed similarly in concert with aridity for all bee guilds and Cactaceae taxa and *L. tridentata*, but the slopes

differed between methods for *Sphaeralcea* taxa (Figure 2.3 A-C). For *Sphaeralcea* taxa,

synchrony increased in less arid conditions for both pairwise phenological synchrony and

community-level metrics of synchrony, but to a greater degree for pairwise synchrony

(Figure 2.3 C).

<u>Co-occurrence and phenological overlap</u>

For bees that are *L. tridentata* specialists and for generalists that visit both

Cactaceae and *Sphaeralcea*, the proportion of taxonomic pairs that co-occurred and were

phenologically synchronous with flowers decreased as conditions became less arid

(Figure 2.4 A-B, Table 2.4 C). In contrast, bees that visit all three plant taxa (Cactaceae,

L. tridentata, and *Sphaeralcea* generalists) were more likely to co-occur and have some

degree of phenological synchrony with flowers when conditions were less-arid (Figure

2.4 C, Table 2.4 C). The proportion of taxonomic pairs that co-occurred and were

phenologically synchronous was not predicted by aridity for Cactaceae specialists,

Sphaeralcea specialists, Cactaceae and *L. tridentata* generalists, or *L. tridentata* and

Sphaeralcea generalists (Figure 2.4 A-B, Table 2.4 C). In contrast to bees, the proportion

of taxonomic pairs that co-occurred and were phenologically synchronous was not

predicted by aridity for any of the three plant taxa (Figure 2.4 C, Table 2.4 C).

Discussion

This study is among the first to examine how aridity is associated with long-term

trends in plant-pollinator phenological synchrony. For most taxa, aridity was a strongly

supported predictor of phenological synchrony between the flight periods of the bee

guilds and the flowering periods of the plants we examined. Phenological synchrony

decreased under more arid conditions, suggesting that increased aridity under climate change could disrupt plant-pollinator interactions. Additionally, across aridity levels generalized bees had higher synchrony with floral resources compared to specialists due to their greater diet breadth. As conditions become more arid in drylands, generalized pollinators could be resilient to reduced overlap with some floral resources, unlike specialists. Given synchrony between flowering and bee flight is critical for the fitness of both partners in these mutualistic interactions, reduced overlap could translate into population declines and reduced pollination services.

Aridification could reduce plant-pollinator phenological synchrony through various physiological mechanisms. For example, extreme heat can shorten the duration of phenophases, making synchrony less likely, especially for specialized solitary bees (Walters & Hassall 2006). Similarly, precipitation can be an important cue that shapes plant and bee phenologies in dryland environments (Danforth 1999; Minckley et al. 2013). Because rainfall typically occurs in pulses in dryland ecosystems (Noy-Meir 1973; Collins et al. 2014), flowering of *L. tridentata* and *Sphaeralcea* taxa and emergence of the bee guilds that pollinate them may be triggered by the same precipitation events, resulting in environmental tracking in their phenologies across space and time (Cane et al. 2005). As larger precipitation events become less common in the drylands studied here (Petrie et al. 2014), this tracking may be disrupted. Although specialized bees are more able to undergo diapause in suboptimal conditions (Minckley et al. 2013), sensitivity to precipitation as a trigger of emergence is not well-understood for the vast majority of bee taxa (Danforth 1999). Some bee species exhibit bet hedging, where only a

fraction of larvae pupate under optimal conditions, which could enable these taxa to maintain phenological synchrony under changing climatic conditions (Danforth 1999; Childs et al. 2010). However, future increases in aridity may erode synchrony as bees and plants may begin to reach their physiological limits under hotter and drier conditions (Kazenel et al. in review). Alternatively, our focal species may be buffered against complete phenological mismatches, as only 207 complete mismatches occurred across the 17,682 possible incidences (1.2%) we examined. Given the lack of long-term data on plant-pollinator phenological synchrony in dryland ecosystems, it is challenging to establish a baseline to predict the implications of phenological asynchrony (Kharouba & Wolkovich 2020), but relatively low degrees of synchrony appear to have maintained population persistence over our time series.

Bees that specialize on Cactaceae flowers and plants within the Cactaceae family were the only taxa that showed increased phenological synchrony with increased aridity. Compared to other focal plant taxa in this study (Atwood & Welsh 2002; Laport et al. 2013), cacti are generally at or near the northern extent of their distributions (Hernández & Gómez-Hinostrosa 2011); thus, more-arid conditions may be more similar to the conditions at the core of their distributions. Additionally, because these taxa are active only during the spring season, they likely do not rely on recent precipitation events to trigger emergence and flowering, whereas the other bee guilds and plant taxa we examined tend to fly and flower in both spring and monsoonal seasons and may be more sensitive to water pulses. Lastly, due to their water storage adaptations in highly arid

conditions (Williams et al. 2014), Cactaceae may be able to continue to flower under increasingly arid conditions.

Many of the expectations about phenological responses may not hold under non-stationary environmental conditions, such as those emerging under climate change (Wolkovich & Donahue 2021). Across the deserts of the southwest, aridity and drought have increased over time (Khatri-Chhetri et al. 2021). In our dryland study site, aridity has increased and precipitation events have generally become smaller, with less time between events during the monsoonal season (Petrie et al. 2014). In the context of long-term directional changes in the climate, particularly the trend towards greater aridity, our results indicate that many plant and bee taxa are likely to have reduced synchrony and therefore reduced interaction strengths. At the same time, these changes in aridity and precipitation patterns will likely lead to increased synchrony between plants in the Cactaceae family and bees that specialize on Cactaceae, potentially impacting community composition and richness under future climates as winners and losers are determined (Prugh et al. 2018).

Diet breadth in bees has been shown to affect phenological distributions and population dynamics (Minckley et al. 2013; Ogilvie & Forrest 2017). Specialists may be under selective pressure to be highly phenologically synchronous with their partners and may therefore be more likely to maintain synchrony under climate change (Rafferty et al. 2015). We, however, did not find significantly different incidences of complete phenological mismatches or transient non-co-occurrence in specialized bee guilds compared to generalists, with specialists averaging 22.0% (+/- 14.6%) non-co-occurrence

and generalists averaging 36.2% (+/- 24.7%) non-co-occurrence with individual partner taxa (Table 2.1 B). Phenological synchrony between taxonomic pairs was also similar between specialized (overlap: 0.31 +/- 0.27) and generalized (overlap: 0.36 +/- 0.30) bees across aridity values. However, when considering community-level phenological synchrony, generalist bees (overlap: 0.67 +/- 0.27) were significantly more synchronous than specialist bees (overlap: 0.44 +/- 0.30), but less synchronous than plants (overlap: 0.93 +/- 0.13) across aridity levels. Greater interaction breadth can improve phenological synchrony, as generalists can potentially interact with a greater richness of floral resources and adaptively forage (Bartomeus et al. 2013; Valdovinos et al. 2013). Our results suggest that specialist bees, in relying on fewer and more closely-related floral resources, may be more vulnerable to becoming asynchronous with the flowering periods of the plants they visit.

Transient non-co-occurrences and complete phenological mismatches likely indicate instances when abiotic cues did not trigger bee and plant emergence and flowering, which may represent an adaptive strategy to avoid activity in seasons or years with unfavorable conditions (Forrest et al. 2019). For example, specialized bees in the southwestern United States are more likely to go into diapause during droughts, and may balance their narrower selection of floral resources with increased synchrony during non-drought seasons, while generalized bees likely become functional specialists as drought narrows their potential partner species breadth (Minckley et al. 2013). However, we did not find differences in the incidence of non-co-occurrences between specialized and generalized bee guilds (Table 2.3 D). Only one generalized bee group (Cactaceae, *L.*

tridentata, and *Sphaeralcea* generalists) had greater proportions of co-occurring and phenologically overlapping taxonomic pairs associated with less-arid conditions. This suggests that, while the degree of synchrony may generally be sensitive to aridity, complete phenological mismatches are not.

Conclusions

Our results show that complete phenological mismatches and the magnitude of phenological overlap from both the bee and plant perspectives could be at risk of worsening as aridity increases in dryland ecosystems. Given the important role that pollination plays in plant reproduction and the dependence of bee reproduction on floral resources, our findings could signal a degradation of ecosystem functioning in a hotter, drier future. Our results are important to predicting future community composition and pollination network structure that can guide the maintenance of pollination services.

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Tables, Images, & Figures

Table 2.1: Bee species included in the study and their floral associations.

Code	Family	Genus	Subgenus	Species	Diet Breadth	Floral partner	Diet breadth citation
APDIAAUS	Apidae	Diadasia		australis	Oligolectic	Cactaceae	KWW, TLG; Sipes & Tepedino 2005
APDIARIN	Apidae	Diadasia		rinconis	Oligolectic	Cactaceae	KWW, TLG; Sipes & Tepedino 2005
ANPERLAR	Andrenidae	Perdita	Perditella	larreae	Oligolectic	Larrea tridentata	KWW, TLG; Minckley et al. 1999; Hurd & Linsley 1975
MEHOPBIS	Megachilidae	Hoplitis	Alcidamea	biscutellae	Oligolectic	Larrea tridentata	KWW; Minckley et al. 1999; Hurd & Linsley 1975
ANMACLAT	Andrenidae	Macrotera	Macroteropsis	latior	Oligolectic	Sphaeralcea	KWW
ANMACPOR	Andrenidae	Macrotera	Macroteropsis	portalis	Oligolectic	Sphaeralcea	KWW, TLG
APDIADIM	Apidae	Diadasia		diminuta	Oligolectic	Sphaeralcea	KWW; Sipes & Tepedino 2005
APDIAMEG	Apidae	Diadasia		megamorpha	Oligolectic	Sphaeralcea	KWW, TLG
APDIAOCH	Apidae	Diadasia		ochracea	Oligolectic	Sphaeralcea	KWW; Sipes & Tepedino 2005
APANTAFF	Apidae	Anthophora	Lophanthophora	affabilis	Polylectic	Cactaceae + Larrea tridentata	TLG
APCENCAE	Apidae	Centris	Paracentris	caesalpiniae	Polylectic	Cactaceae + Larrea tridentata	KWW
HAAGAMEL	Halictidae	Agapostemon		melliventris	Polylectic	Cactaceae + Larrea tridentata	KWW, TLG; Minckley et al. 1999; Hurd & Linsley 1975; Hurd et al. 1980
MEASHCAC	Megachilidae	Ashmeadiella	Ashmeadiella	cactorum	Polylectic	Cactaceae + Larrea tridentata	KWW, TLG; Minckley et al. 1999
APANTCAL	Apidae	Anthophora	Anthophoroides	californica	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW; Hurd & Linsley 1975
APANTURB	Apidae	Anthophora	Mystacanthophora	urbana	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW, TLG; Minckley et al. 1999; Hurd & Linsley 1975
HAAGAANG	Halictidae	Agapostemon		angelicus	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW, TLG; Minckley et al. 1999; Hurd & Linsley 1975; Hurd et al. 1980
HAHALLIG	Halictidae	Halictus		ligatus	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW, TLG; Hurd et al. 1980
HAHALTRI	Halictidae	Halictus		tripartitus	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW, TLG; Hurd et al. 1980
HALASSEM	Halictidae	Lasioglossum	Dialictus	semicaeruleum	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	TLG

HALASSIS	Halictidae	Lasioglossum	Lasioglossum	sisymbrii	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW; Minckley et al. 1999; Hurd & Linsley 1975; Hurd et al. 1980
MEASHMEL	Megachilidae	Ashmeadiella	Ashmeadiella	meliloti	Polylectic	Cactaceae + Larrea tridentata + Sphaeralcea	KWW, TLG
APMESPAR	Apidae	Melissodes	Melissodes	paroselae	Polylectic	Cactaceae + Sphaeralcea	KWW; Hurd & Linsley 1975; Hurd et al. 1980
MEMEGSUB	Megachilidae	Megachile	Megachiloides	sublaurita	Polylectic	Cactaceae + Sphaeralcea	KWW
ANPERCAL	Andrenidae	Perdita	Hexaperdita	callicerata	Polylectic	Larrea tridentata + Sphaeralcea	KWW
ANPERMAR	Andrenidae	Perdita	Perditella	marcialis	Polylectic	Larrea tridentata + Sphaeralcea	KWW, TLG; Hurd & Linsley 1975
APMESTRI	Apidae	Melissodes	Eumelissodes	tristis	Polylectic	Larrea tridentata + Sphaeralcea	KWW, TLG; Minckley et al. 1999; Hurd & Linsley 1975; Hurd et al. 1980
MEANTPOR	Megachilidae	Anthidium	Anthidium	porterae	Polylectic	Larrea tridentata + Sphaeralcea	TLG

Table 2.2: Summary of species and interaction richness for bee guilds and plant taxa.

Bee guild visitation	Num. Potential species	Num. Abundant species	Percent abundant species (%)	Num. Partner species	Potential interactions
Cactaceae	5	2	40	8	672
Larrea	8	2	25	1	84
Sphaeralcea	12	5	42	4	840
C+L	7	3	43	9	1134
C+L+S	11	8	73	13	4368
C+S	2	2	100	12	1008
L+S	12	4	33	5	840
Plant taxa					
Cactaceae	19	8	42	14	4704
Larrea	1	1	100	16	672
Sphaeralcea	6	4	67	20	3360

Bee guild visitation	Missing interactions	Realized interactions	Synchronous interactions	Mismatches	Mean synchrony
Cactaceae	542	130	130	0	0.318
Larrea	52	32	31	1	0.57
Sphaeralcea	629	211	208	3	0.367
C+L	940	194	183	11	0.321
C+L+S	3320	1048	993	55	0.304
C+S	896	112	89	23	0.251
L+S	565	275	271	4	0.422
Plant taxa					
Cactaceae	3959	745	722	23	0.424
Larrea	283	389	380	9	0.374
Sphaeralcea	2303	1057	979	78	0.361

Table 2.3: Comparing AIC values between candidate models with varying lags of pre-phenophase SPEI (standardized evapotranspiration index).

Name	Taxa	Predictor	dAIC	DF
Cactaceae specialist bees	Specialist	SPEI during flight period	0	8
Cactaceae specialist bees	Specialist	SPEI 6 months prior to flight period	10.8397735	8
Cactaceae specialist bees	Specialist	SPEI 2 months prior to flight period	11.5443812	8
Cactaceae specialist bees	Specialist	SPEI 3 months prior to flight period	12.8825483	8
Cactaceae specialist bees	Specialist	SPEI 1 month prior to flight period	12.9181012	8
L. tridentata specialist bees	Specialist	SPEI during flight period	0	7
L. tridentata specialist bees	Specialist	SPEI 2 months prior to flight period	0.71668796	7
L. tridentata specialist bees	Specialist	modresults[[1]]	1.30470889	7
L. tridentata specialist bees	Specialist	SPEI 6 months prior to flight period	1.76576132	7
L. tridentata specialist bees	Specialist	SPEI 3 months prior to flight period	1.88080758	7
Sphaeralcea specialist bees	Specialist	SPEI during flight period	0	7
Sphaeralcea specialist bees	Specialist	SPEI 3 months prior to flight period	11.1960965	7
Sphaeralcea specialist bees	Specialist	SPEI 2 months prior to flight period	15.3924818	7
Sphaeralcea specialist bees	Specialist	SPEI 6 months prior to flight period	20.0196208	7
Sphaeralcea specialist bees	Specialist	SPEI 1 month prior to flight period	22.0388134	7
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 6 months prior to flight period	0	7
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 1 month prior to flight period	5.16789546	7
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 2 months prior to flight period	5.65311775	7
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 3 months prior to flight period	7.47099519	7
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI during flight period	7.74054195	7
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	0	7

Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI 6 months prior to flight period	13.109895	7
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI 2 months prior to flight period	14.3206749	7
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI 3 months prior to flight period	15.4434012	7
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI 1 month prior to flight period	15.6703463	7
Cactaceae and *Sphaeralcea* generalist bees	Specialist	SPEI during flight period	0	8
Cactaceae and *Sphaeralcea* generalist bees	Specialist	SPEI 6 months prior to flight period	2.99264845	8
Cactaceae and *Sphaeralcea* generalist bees	Specialist	SPEI 1 month prior to flight period	3.41220842	8
Cactaceae and *Sphaeralcea* generalist bees	Specialist	SPEI 3 months prior to flight period	4.01550728	8
Cactaceae and *Sphaeralcea* generalist bees	Specialist	SPEI 2 months prior to flight period	4.10057285	8
L. tridentata and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	0	7
L. tridentata and *Sphaeralcea* generalist bees	Generalist	modresults[[2]]	6.53751031	7
L. tridentata and *Sphaeralcea* generalist bees	Generalist	SPEI 6 months prior to flight period	7.24959426	7
L. tridentata and *Sphaeralcea* generalist bees	Generalist	modresults[[1]]	7.29782709	7
L. tridentata and *Sphaeralcea* generalist bees	Generalist	SPEI 3 months prior to flight period	7.91004663	7
Cactaceae	Plant	SPEI 6 months prior to flowering	0	7
Cactaceae	Plant	SPEI 3 months prior to flowering	2.95057882	7
Cactaceae	Plant	SPEI during flowering	3.07173049	7
Cactaceae	Plant	SPEI 1 month prior to flowering	3.91846458	7
Cactaceae	Plant	SPEI 2 months prior to flowering	4.66154257	7
L. tridentata	Plant	SPEI 2 months prior to flowering	0	7
L. tridentata	Plant	SPEI 3 months prior to flowering	1.06505858	7
L. tridentata	Plant	SPEI 6 months prior to flowering	3.65960318	7
L. tridentata	Plant	SPEI 1 month prior to flowering	5.50317712	7
L. tridentata	Plant	SPEI during flowering	5.65923366	7

		SPEI 6 months prior to flowering	0	7
Sphaeralcea	Plant	SPEI 3 months prior to flowering	0.417264	7
Sphaeralcea	Plant	SPEI 2 months prior to flowering	10.1354898	7
Sphaeralcea	Plant	SPEI 1 month prior to flowering	19.1380986	7
Sphaeralcea	Plant	SPEI during flowering	21.1368586	7

Table 2.4: Model results for bee guilds and plants taxa. A) Model results for species-level phenological synchrony predicted by aridity (Standardized precipitation evapotranspiration index; SPEI). The lag for SPEI (period during phenophase, or 2, 3, 6, or 9 months prior to a species' phenophase in a given year and site) was determined using AIC values. B) Model results comparing phenological synchrony between species and community level analyses, predicted by aridity, analysis method (species vs community level), and an interaction of the two. Aridity (SPEI) was selected using the same method as in A). C) Model results for quantifying co-occurrence of a given bee or plant focal taxa with their interaction partners. Aridity (SPEI) was selected using the same methodology as above. D) Model comparing species co-occurrence between specialist and generalist bee guilds.

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A) Species-level phenological synchrony						
Name	Taxa	Predictor	Estimate	Std error	Z value	P value
Cactaceae specialist bees	Specialist	SPEI during flight period	-2.1278	0.5282	-4.0287	<0.001
L. tridentata specialist bees	Specialist	SPEI during flight period	1.0471	0.767	1.3652	0.1722
Sphaeralcea specialist bees	Specialist	SPEI during flight period	2.5576	0.5817	4.3969	<0.001
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 6 months prior to flight period	1.7866	0.6023	2.9663	0.003
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	1.0812	0.2826	3.8265	<-0.001
Cactaceae and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	1.1948	0.5622	2.1252	0.0336
L. tridentata and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	1.3537	0.4999	2.7083	6.80E-03
Cactaceae	Plant	SPEI 6 months prior to flowering	-0.5891	0.2735	-2.1539	0.0312
L. tridentata	Plant	SPEI 2 months prior to flowering	0.9147	0.3653	2.5038	0.0123
Sphaeralcea	Plant	SPEI 6 months prior to flowering	1.1035	0.2332	4.73E+00	<0.001

B) Comparing species and community level synchrony					
		Term	Statistic	Degrees of freedom	P value
Cactaceae specialist bees	Specialist	SPEI during flight period	11.6381387	1	0.00064613
Cactaceae specialist bees	Specialist	Analysis method	11.1995141	2	0.00369876
Cactaceae specialist bees	Specialist	SPEI during flight period * Analysis method	0.00010783	1	0.99171488
L. tridentata specialist bees	Specialist	SPEI during flight period	10.8144753	1	1.01E-03
L. tridentata specialist bees	Specialist	Analysis method	0.7855046	2	0.67519597
L. tridentata specialist bees	Specialist	SPEI during flight period * Analysis method	1.63E-05	1	0.99677559
Sphaeralcea specialist vees	Specialist	SPEI during flight period	63.4569358	1	1.64E-15

Sphaeralcea specialist vees	Specialist	Analysis method	8.36344695	2	0.01527216
Sphaeralcea specialist vees	Specialist	SPEI during flight period * Analysis method	0.15721559	1.00E+00	0.6917331
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 6 months prior to flight period	6.61204887	1	1.01E-02
Cactaceae and *L. tridentata* generalist bees	Generalist	Analysis method	126.979623	2	2.67E-28
Cactaceae and *L. tridentata* generalist bees	Generalist	SPEI 6 months prior to flight period * Analysis method	3.54499153	1	5.97E-02
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	47.1309878	1	6.64E-12
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	Analysis method	1067.90962	2	1.28E-232
Cactaceae, *L. tridentata*, and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period * Analysis method	0.00085102	1.00E+00	0.97672719
Cactaceae and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	5.45008089	1	1.96E-02
Cactaceae and *Sphaeralcea* generalist bees	Generalist	Analysis method	132.171457	2	1.99E-29
Cactaceae and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period * Analysis method	1.06689465	1	0.30164793
L. tridentata and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period	15.813843	1	6.99E-05
L. tridentata and *Sphaeralcea* generalist bees	Generalist	Analysis method	49.5956872	2	1.70E-11
L. tridentata and *Sphaeralcea* generalist bees	Generalist	SPEI during flight period * Analysis method	2.11279117	1	0.14607268
Cactacea	Plant	SPEI 6 months prior to flowering	18.5791542	1	1.63E-05
Cactacea	Plant	Analysis method	760.690668	2	6.58E-166
Cactacea	Plant	SPEI 6 months prior to flowering * Analysis method	1.13070698	1	0.28762459

Name	Taxa	Predictor	Estimate	Std error	Z value	P value
L. tridentata	Plant	SPEI 2 months prior to flowering	5.07767855		1	2.42E-02
L. tridentata	Plant	Analysis method	829.701349		2	6.80E-181
L. tridentata	Plant	SPEI 2 months prior to flowering * Analysis method	0.0868789		1	0.76818313
Sphaeralcea	Plant	SPEI 6 months prior to flowering	39.3095578		1	3.62E-10
Sphaeralcea	Plant	Analysis method	1656.40426		2.00E+00	0.00E+00
Sphaeralcea	Plant	SPEI 6 months prior to flowering * Analysis method	5.96535431		1	0.01458967

C) Co-occurrence and phenoloical overlap

Name	Taxa	Predictor	Estimate	Std error	Z value	P value
Cactaceae specialist bees	Specialist	SPEI 2 months prior to flight period	-0.2113	0.4593	-0.46	0.6455
L. tridentata specialist bees	Specialist	SPEI 3 months prior to flight period	-2.825	0.9987	-2.8287	0.0047
Sphaeralcea specialist vees	Specialist	SPEI 1 month prior to flight period	0.3963	0.5811	0.682	0.4953
Cactaceae and L. tridentata generalist bees	Generalist	SPEI 3 months prior to flight period	-0.4989	0.7113	-0.7013	0.4831
Cactaceae, L. tridentata, and Sphaeralcea generalist bees	Generalist	SPEI 6 months prior to flight period	0.6698	0.3105	2.1572	0.031
Cactaceae and Sphaeralcea generalist bees	Generalist	SPEI 1 month prior to flight period	-2.1375	0.4576	-4.6716	<0.001
L. tridentata and Sphaeralcea generalist bees	Generalist	SPEI 6 months prior to flight period	0.7272	0.3802	1.9127	0.0558
Cactaceae	Plant	SPEI 2 months prior to flowering	-0.608	0.5207	-1.1676	0.243
L. tridentata	Plant	SPEI 1 month prior to flowering	1.0558	0.7267	1.4528	0.1463
Sphaeralcea	Plant	SPEI 3 months prior to flowering	0.5409	0.4872	1.1102	0.2669

D) Co-occurrence and phenological overlap: comparing specialist and generalist bee guilds

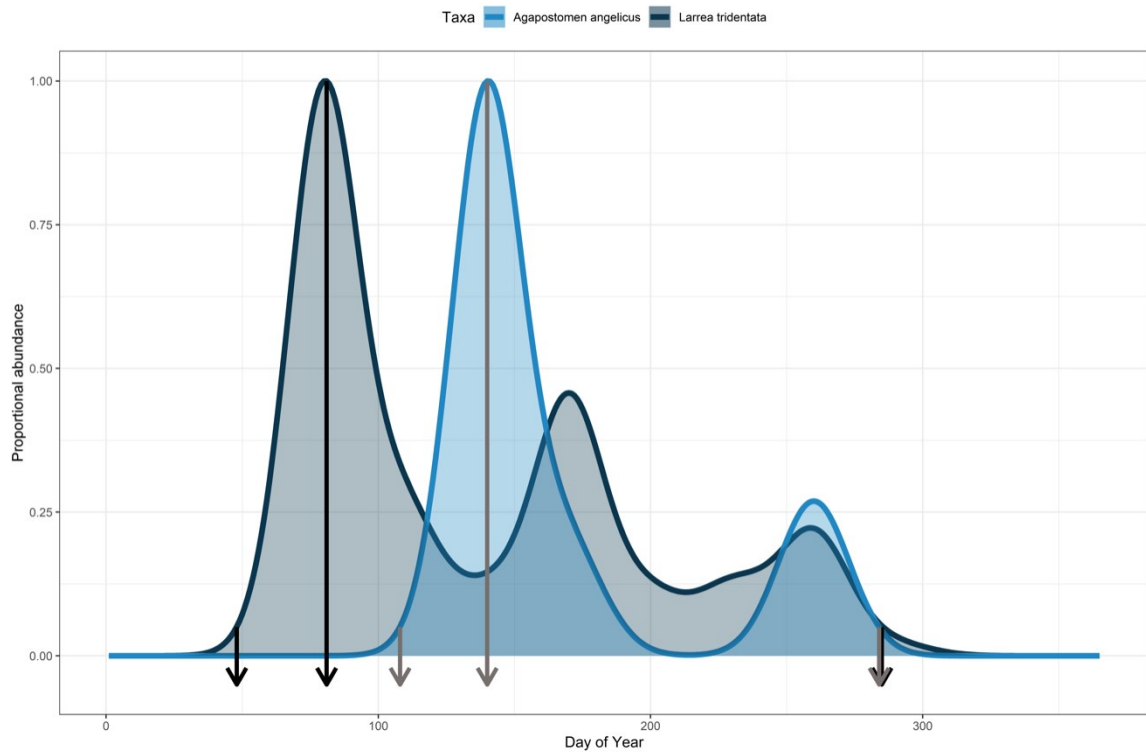|		Predictor	Estimate	Std error	Z-value	P value
		Diet breath (specialist vs. generalist)	0.745	0.1315	5.711	<0.001

Figure 2.1: Example phenological distributions of *Larrea tridentata* and *Agapostemon angelicus* (generalist bee) constructed using circular density distributions. The dark blue area represents phenological overlap. To quantify synchrony, the overlapping area was divided by the total area under the curve for each species, resulting in two unique metrics of phenological synchrony. Black (representing *L. tridentata*), and grey (representing *Agapostemon angelicus*) arrows indicate phenological emergence, peak, and senescence.

Figure 2.2: Phenological synchrony generally increased in association with aridity (standardized precipitation-evapotranspiration index: SPEI) for (A) specialist bee guilds, (B) generalist bee guilds visiting Cactaceae and *Larrea tridentata* (C+L), Cactaceae, *Larrea tridentata*, and *Sphaeralcea* (C+L+S), Cactaceae and *Sphaeralcea* (C+S), and *Larrea tridentata* and *Sphaeralcea* (L+S), and (C) plant taxa. Pre-phenophase SPEI (1, 2, 3, 6, and 12 month windows) and phenophase SPEI were selected using AIC to determine best fit. Asterisks in x-axis indicate significance.

Figure 2.3: Phenological synchrony for species pairs (light blue) and between a species and its entire potential community of interacting partners (dark blue) in response to standardized precipitation-evapotranspiration index (SPEI) for (A) specialist bee guilds, (B) generalist bee guilds visiting Cactaceae and *Larrea tridentata* (C+L), Cactaceae, *Larrea tridentata*, and *Sphaeralcea* (C+L+S), Cactaceae and *Sphaeralcea* (C+S), and *Larrea tridentata* and *Sphaeralcea* (L+S), and (C) plant taxa. Pre-phenophase SPEI (1, 2, 3, 6, and 12 month windows) and phenophase SPEI were selected using AIC to determine best fit.

Figure 2.4: The proportion of co-occurring and phenologically overlapping species pairs out of the maximum number of potentially interacting species pairs (transiently non co-occurring species pairs + completely phenologically mismatched species pairs + co-occurring and phenologically overlapping species pairs) against standardized precipitation-evapotranspiration index (SPEI) for (A) specialist bee guilds, (B) generalist bee guilds visiting Cactaceae and *Larrea tridentata* (C+L), Cactaceae, *Larrea tridentata*, and *Sphaeralcea* (C+L+S), Cactaceae and *Sphaeralcea* (C+S), and L*arrea tridentata* and *Sphaeralcea* (L+S), and (C) plant taxa. Pre-phenophase SPEI (1, 2, 3, 6, and 12 month windows) and phenophase SPEI were selected using AIC to determine best fit. Asterisks in x-axis indicate significance.
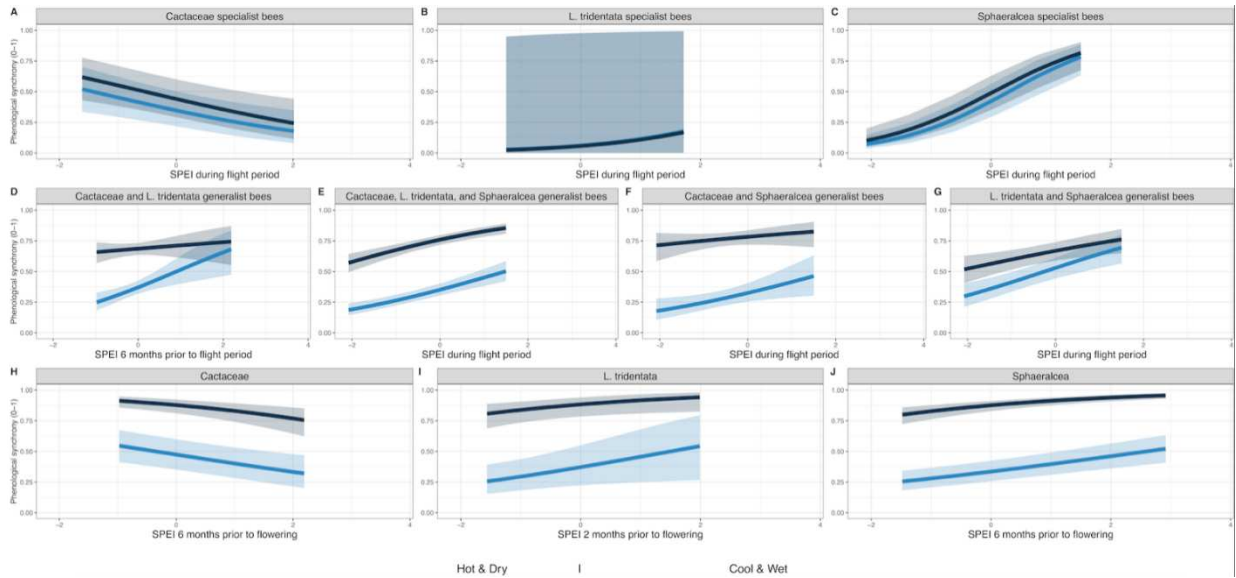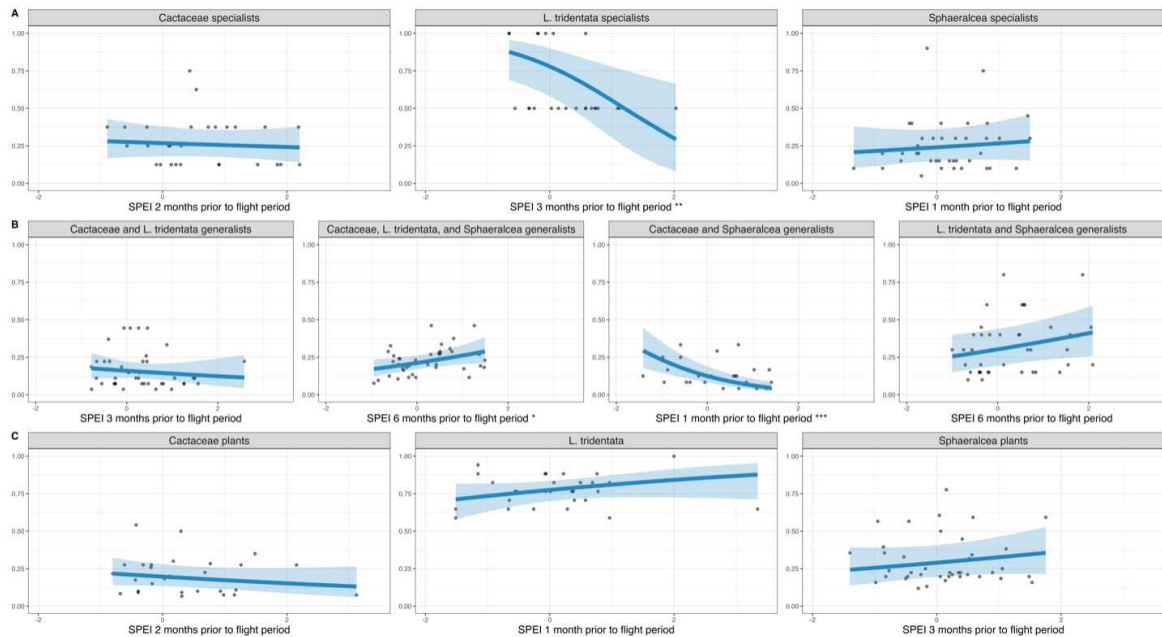
Chapter 3

Experimental biomass reduction alters flowering synchrony in a montane dryland ecosystem

Abstract

As climate change alters net primary production (NPP) of terrestrial plant communities, flowering phenology is also likely to be altered. Flowering synchrony of conspecific and heterospecific neighbors in a community can impact competition and facilitation, affecting processes such as pollination. Plant communities in drylands may be particularly vulnerable to drought-induced reductions in NPP and mortality as climates become more arid. We experimentally reduced approximately 50% of aboveground plant biomass on a per species basis at three sites (subalpine, alpine transition, and alpine) along a dryland elevational gradient and measured how the probability of flowering and flowering synchrony differed between manipulated and control plots. Plants at the highest elevation alpine site had a greater probability of flowering in the manipulated plots. Conspecific flowering synchrony was greater in reduced-biomass plots across all sites, whereas heterospecific co-flowering synchrony was significantly lower in reduced-biomass plots in the subalpine and alpine transition sites and did not differ at the alpine site. These findings suggest that reduced plant biomass associated with drought-induced stress could alter local community-level flowering phenology, potentially bolstering gene flow between nearby conspecifics and reducing the richness of floral resources available simultaneously to pollinators under climate change.

Introduction

Climate change impacts the productivity of plants within communities (Becklin et al. 2016; Vitasse et al. 2021; Inouye 2022). Net primary production (NPP) in dryland and alpine ecosystems has generally declined due to increased duration and intensity of droughts (Gherardi & Sala 2019; Xu et al. 2020). Climate change-induced reductions in NPP are likely to affect both the probability and timing of flowering, with indirect effects extending to neighboring plants as competitive and facilitative interactions are altered. Flowering is energetically expensive, and plants often reduce resource allocation to reproduction under stress (Teixido & Valladares 2014; Bourbia et al. 2020). Similarly, higher temperatures can scale up to reduce floral abundance at the landscape level (Aldridge et al. 2011). Thus, plants may be less likely to flower and to have altered flowering phenology in response to community-level reductions in NPP. As a result, the synchrony of flowering between conspecific (Ison & Wagenius 2014) and heterospecific plants (Wolf et al. 2017; Arceo-Gómez 2021) may be changed.

Changes in flowering patterns are likely to affect plant population dynamics (Iler et al. 2021). For example, reduced biomass may translate into the production of fewer, smaller flowers that produce less nectar and pollen at the community level (Galen 2000; Kuppler et al. 2021). Lower quantity and quality of floral resources can then lead to reduced pollination success (Kuppler et al. 2021). The degree of flowering synchrony can shape competition or facilitation between individuals via its effects on pollinator behavior (Bergamo et al. 2020; Albor et al. 2022). Low levels of synchrony in the flowering of conspecifics, termed flowering synchrony, can reduce the likelihood of pollen transfer by

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pollinators, reducing gene flow and reproductive success (Hall et al. 2018; Rivest et al. 2021; Schiffer et al. 2023). High degrees of synchrony in the flowering of heterospecifics, termed co-flowering synchrony, can increase heterospecific pollen deposition, which can decrease pollination success (Vilela et al. 2018; Waters et al. 2020). Finally, altered flowering patterns that stem from reductions in plant biomass may also impact insect pollinator population dynamics, which can be shaped by availability of floral resources (Ogilvie & Forrest 2017).

In this study, we tracked the floral abundance and flowering phenology of more than 800 individual plants of 28 species at three sites along a dryland subalpine-alpine elevation gradient after experimentally reducing aboveground plant biomass. We hypothesized that plants in plots with reduced aboveground biomass would have both a lower probability of flowering and lower flowering and co-flowering synchrony compared to plants in unmanipulated plots, and that these differences would be greatest at the lowest elevation subalpine site where aridity was highest.

Methods

Study sites

This study was conducted in summer 2019-2021 in the White Mountains of California in the Inyo National Forest, Mono County, California. The White Mountains lie in the rain shadow of the Eastern Sierra, and receive about one third of the precipitation as sites at the same elevations in the Eastern Sierra (Hall, Jr. 1991). Most precipitation comes as winter snowfall, with additional monsoonal precipitation during the summer. Monthly summer weather conditions (June-September) during the three

years of the study period averaged 11.1 C (+/- 2.3 C) and 1.6 cm (+/- 2.5 cm) of precipitation in the subalpine zone (Crooked Creek Laboratory; Subalpine site) and 7.2 C (+/- 2.4 C) and 9.7 cm (+/- 8.2 cm) of precipitation in the alpine zone (Barcroft Laboratory; Alpine site). The flora includes more than 130 species in the subalpine habitats dominated by sage scrub, and 163 vascular species in the alpine zone (Hall, Jr. 1991; Rundel 2011).

In the winter of 2018-19, the White Mountains experienced an exceptional amount of snowfall, with snowpack remaining well into August in the fellfields at elevations of 3900 m. In 2020 and 2021, the White Mountains received very little winter or summer precipitation, resulting in a state of exceptional drought during the summer of 2021 ("Time Series | U.S. Drought Monitor" 2023). Beginning in June 2021, the White Mountains experienced higher than average monsoonal precipitation, lessening the drought status of the subalpine and alpine zones.

Our study consisted of three sites, with 4-6 plots per site (Figure 3.1). The subalpine site (37.486581, -118.185947) was at the lowest elevation (3170 m) in a subalpine sage scrub meadow dominated by *Artemesia rothrockii* (Asteraceae) with a rich community of small forbs. There was a total of 17 flowering species across the six plots at the subalpine site. The alpine transition site (3550 m; 37.561152, -118.231989) had a lower density of *A. rothrockii* compared to the subalpine site, and consisted of both subalpine and alpine species, with 17 flowering species across the six plots. The alpine site (3900 m; 37.583532, -118.242640), was located in an alpine fellfield in the saddle east of Barcroft Peak and had a total of 10 flowering species across four plots.

Data collection

We established the sites and plots in June 2019. In 2019, we identified every individual flowering plant within each of the 2 x 2 m plots and noted if each plant flowered during the season. The location of each individual plant was recorded using within-plot coordinates and marked with a colored toothpick. We were unable to consistently collect data in 2020 because of COVID-19 mitigation protocols at the White Mountain Research Center, and we therefore are not using the limited data from that field season. In 2021, we tracked flowering for individual plants. Starting at flowering onset, we recorded the number of open flowers every 2-5 days for the duration of the flowering period. Flowers of species for which individual plants were difficult to distinguish were summed across the entire plot. Flowering began in mid June and continued through August.

Biomass manipulation

After all flowers had senesced in 2019, we performed an aboveground biomass manipulation in one plot in each pair of plots at each site. We removed approximately 50% of the aboveground biomass in each manipulated plot on a per-species basis. First, we identified every plant in each plot, and measured the length (l) and width (w) of living plant matter. Based on an ellipse using plant length and width, we estimated the percent of each plant that was not living (pd) in order to better estimate plant biomass. We then calculated the area of each individual plant in cm^2 ($\pi*l*w*(1-pd)$) to estimate aboveground biomass. We used the estimated biomass to rank plants of each species by their area, and selected every other plant by rank for biomass removal. We continued this process for each species until 50% of the estimated aboveground biomass was removed.

For species for which individual plants were difficult to distinguish based on aboveground growth, we removed 50% of the aboveground biomass based on the estimated ground cover within the plots (Table 3.1). At the beginning of the 2020 and 2021 flowering seasons, we cut back new growth on plants from which biomass had previously been removed; thus plants from which biomass was removed were not allowed to flower during the study. We re-measured the same plants at the end of the 2021 season.

<u>Flowering probability and synchrony</u>

We first determined the flowering probability of each of the 857 plants that flowered between 2019 and 2021. Only 207 of the 857 plants from 16 of 28 species flowered in 2021, excluding the plants that were removed during the biomass reduction. Of the 207 plants, 98 plants flowered both years, with 109 plants flowering in 2021 but not 2019. Plants that bloomed in 2020 were excluded from the analyses. Plants that flowered in 2021 were coded 1, and plants that flowered in 2019 but not 2021 were coded 0. We used this binomial data to first determine how flowering probability changed post-manipulation.

Using the subset of individual plants that flowered in 2021, we determined flowering synchrony with conspecific plants within each plot and co-flowering synchrony with heterospecific plants within each plot. We imputed daily resolution phenological distributions for each plant using von Mises kernel density from the 'densityFit' function (Ridout & Linkie 2009). We selected bandwidth sensitivity using the vm.kde function in

the package Direction, with the average bandwidth being 467 (Tsagris et al. 2023). This produced daily phenological distributions for each plant.

To quantify synchrony, we compared the phenological distributions of each plant to every other plant within a given plot. We then quantified the overlapping area of the two phenological distributions to the total area under the distribution of both plants (Figure 3.2). This yielded, for each pair of plants within a plot, one metric of phenological synchrony that ranged from 0 (asynchrony) to 1 (complete synchrony). We separated phenological synchrony into values between individual plants of the same species (flowering synchrony) and between individual plants of different species (co-flowering synchrony).

Data analyses

We quantified how the probability of flowering was predicted by site, treatment, and their interaction using the binomial flowering data. We used a generalized linear model with a binomial error distribution and logit-link in the R the package glmmTMB (Brooks et al. 2017). We tested for residual normality, dispersion, and the presence of outliers using the R package DHARMa and found the model met all assumptions (Hartig & Lohse 2022).

Similarly, we modeled flowering synchrony and co-flowering synchrony, testing how each was predicted by site, treatment, and their interaction. We used generalized linear models with an ordered beta error distribution and logit-link in glmmTMB (Brooks et al. 2017; Kubinec 2022). The models met the assumptions of residual normality, dispersion, and outliers.

Figures were produced using ggplot2 and the ggpredict function in ggeffects and all analyses were conducted in R (Wickham 2009; Lüdecke 2018; R Core Team 2020).

Results

Generally, only a small ratio of plants flowered in 2021 compared to 2019, ranging from 11.6% to 100% in control plots, and 0% to 370% in reduced biomass plots (Table 3.1). There was a higher probability of flowering in reduced biomass plots at the alpine site, while the probability of flowering was not different between control and reduced biomass plots at the subalpine and alpine transition sites (Table 3.2 A; Figure 3.3 A).

Flowering synchrony was significantly higher for reduced biomass plots at all sites compared to control plots (Table 3.2; Figure 3.3 B). There was no significant difference in flowering synchrony between sites for either reduced biomass or control plots (Table 3.2 B; Figure 3.3 B).

Reduced biomass plots had significantly lower degrees of co-flowering synchrony compared to control plots at the subalpine and alpine transition sites (Table 3.2 C; Figure 3.2 C). The alpine site had similar degrees of co-flowering synchrony compared to the lower sites, and did not differ between control and reduced biomass plots (Table 3.2 C; Figure 3.3 C).

Discussion

Biomass reduction altered the dynamics of flowering in plant communities across the elevational gradient in this study. In high elevation alpine communities, plants in reduced biomass plots were more likely to flower. Across all sites, plants in reduced

biomass plots had higher flowering synchrony compared to control plots. At the lower two sites, biomass reduction resulted in lower co-flowering synchrony. Together, these results indicate that reduced aboveground plant biomass could reshuffle the flowering phenologies of plant communities under more arid conditions and increased drought-induced mortality.

Reduced biomass plots had higher degrees of flowering synchrony while having lower or comparable degrees of co-flowering synchrony. As drought decreases NPP and ground cover in dryland ecosystems, soil moisture is expected to decrease due to elevated evaporation of base soils (D'Odorico et al. 2007; Berdugo et al. 2020, 2022). Increased temperatures and drought can cause species-specific changes in phenology, potentially increasing within-species phenological synchrony as species have different phenological sensitivity and express less phenotypic plasticity to allocate limited resources towards flowering (Bongers et al. 2017; Rice et al. 2021; Flores et al. 2023). Reduced biomass could therefore lead to increased flowering synchrony via decreased soil moisture availability. Additionally, reduced soil moisture availability could cause plants to stagger their flowering times to avoid competition for resources (Berger & Ludwig 2014). More staggered flowering phenologies among species, along with longer flowering seasons due to earlier snowmelt and warmer spring temperatures (Stewart et al. 2004), could explain the simultaneous decrease in heterospecific co-flowering synchrony and increased conspecific flowering synchrony. These trends in flowering and co-flowering synchrony are similar to those found in a semi-arid ecosystem, where reductions in co-flowering synchrony were associated with increased temperatures (Fisogni et al. 2022).

Higher degrees of flowering synchrony can increase conspecific pollen transfer and reproductive success (Ison et al. 2014; Gleiser et al. 2018; Hall et al. 2018). Flowering synchrony increases the likelihood of pollinators depositing pollen from one conspecific neighbor to another. Given the small spatial scale used in this study, increased flowering synchrony may have improved the likelihood of such pollen deposition. While drought stress can impact seed quality directly (Alqudah et al. 2011) and indirectly through impacts on pollinators and pollination (Rering et al. 2020), the potential for increased pollination success due to increased flowering synchrony may augment plant reproductive success under climate change.

Decreased co-flowering synchrony could similarly bolster pollination services as climate change decreases NPP. Decreased flowering synchrony can result in less heterospecific pollen deposition, which can increase reproductive success (Morales & Traveset 2008). Co-flowering can also improve heterospecific facilitation to attract more pollinators to rare plants (Bizecki Robson 2013), so the implications of decreasing co-flowering synchrony in this system likely depend on pollinator abundance and richness (Ye et al. 2014). The lack of differentiation in co-flowering synchrony between control and reduced biomass plots at the highest site could mean that the flowering season in the alpine is not long enough for plants to stagger their phenology (Chen et al. 2023), and so competition for pollinators there could remain high compared to the lower sites.

From the pollinator perspective, the effects of decreased flowering probability and altered flowering phenology are likely to be variable. Decreased flower abundance and shifts in phenology are linked to declining pollinator populations (Ogilvie et al. 2017).

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For the pollinator populations that persist through drought conditions, decreased co-flowering synchrony could close gaps between the flowering periods of different species. This could be especially beneficial for pollinators with short foraging and nesting seasons, which likely have a greater risk of phenological asynchrony (Memmott et al. 2007; Rafferty et al. 2015). However, increased conspecific flowering synchrony could increase the likelihood of phenological asynchrony by narrowing the window of time for interaction. The combined effects of decreased flower production (Aldridge et al. 2011) and floral nutrition (Rering et al. 2020; Wilson Rankin et al. 2020) could outweigh the benefits of greater plant-pollinator phenological synchrony (de Manincor et al. 2023), but the relative importance of these impacts on pollinator populations remains to be explored.

In conclusion, reduced aboveground plant biomass led to changes in flowering synchrony within and between species at a local scale along a subalpine-alpine gradient. As climate change and drought reduce NPP and plant biomass, shifts in flowering phenology that increase conspecific pollen deposition and decrease heterospecific competition for pollinators could buffer decreased flowering probability to maintain pollination. As aridification threatens plant and pollinator populations globally, these results could represent a small silver lining for the most drought resistant plants species in montane dryland ecosystems.

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Tables, Images, & Figures

Table 3.1: Summary of plots at subalpine, alpine transition, and alpine sites in the study. Comparison of pre-and post-manipulations of species richness, number of flowering plants, ratio of flowering plants, mean flowering onset, peak and senescence in day of year.

Site	Plot	Elevation (m)	Pre/Post-manipulation	Species richness	Flowering plants removed	# flowering plants	Proportion of flowering plants post-manipulation	Mean flr onset	Mean flr peak	Mean flr senescence
Alpine	C1	3900	Pre	5		74		190	199	206
			Post	3		14	0.189	183	191	201
	M1	3900	Pre	6	12	36		196	200	205
			Post	4		11	0.458	180	188	199
	C2	3890	Pre	7		43		198	204	212
			Post	2		5	0.116	178	185	201
	M2	3890	Pre	7	4	14		211	215	219
			Post	3		37	3.7	184	195	210
Alpine transition	C1	3555	Pre	5		21		199	207	219
			Post	4		21	1	206	213	222
	M1	3550	Pre	4	18	46		199	205	213
			Post	4		21	0.75	177	189	205
	C2	3540	Pre	4		6		209	212	215
			Post	1		1	0.167	192	194	196
	M2	3540	Pre	3	3	11		210	218	227
			Post	3		7	0.875	185	201	213
	C3	3560	Pre	3		21		196	204	213
			Post	1		5	0.238	177	199	238
	M3	3560	Pre	8	7	32		202	207	214
			Post	2		5	0.2	188	190	193

Subalpine	C1	3180	Pre	9		130		190	199	210
			Post	7		35	0.269	197	202	209
	M1	3180	Pre	8	46	116		192	200	210
			Post	3		33	0.471	216	222	228
	C2	3175	Pre	4		24		190	202	221
			Post	1		3	0.125	203	212	228
	M2	3170	Pre	6	14	31		187	199	216
			Post	1		1	0.059	218	219	220
	C3	3185	Pre	4		36		192	199	210
			Post	1		8	0.222	193	201	207
	M3	3185	Pre	3	5	13		188	197	214
			Post	0		0	0			

Table 3.2: Summary of plots at subalpine, alpine transition, and alpine sites in the study. Comparison of pre-and post-manipulations of species richness, number of flowering plants, proportion of flowering plants, mean flowering onset, peak and senescence. EMM (estimated marginal means) grouping indicates which groups are significantly different from one another (P < 0.05).

A. Probability of flowering						
Site	Treatment	Estimated marginal mean	Standard error	Lower confidence interval	Upper confidence interval	EMM group
Alpine	Control	0.21	0.21	0.15	0.29	a
	Reduced biomass	0.64	0.23	0.53	0.73	d
Alpine transition	Control	0.56	0.23	0.45	0.67	cd
	Reduced biomass	0.54	0.21	0.46	0.65	cd
Subalpine	Control	0.31	0.14	0.25	0.37	ab
	Reduced biomass	0.38	0.18	0.30	0.46	bc
B. Flowering synchrony						
Site	Treatment	Estimated marginal mean	Standard error	Lower confidence interval	Upper confidence interval	EMM group
Alpine	Control	0.12	0.15	0.09	0.15	a
	Reduced biomass	0.26	0.06	0.24	0.28	b
	Control	0.12	0.13	0.10	0.15	a

Alpine transition	Reduced biomass	0.32	0.10	0.28	0.36	b
Subalpine	Control	0.09	0.07	0.08	0.10	a
	Reduced biomass	0.29	0.05	0.27	0.31	b

C. Co-flowering synchrony						
Site	**Treatment**	**Estimated marginal mean**	**Standard error**	**Lower confidence interval**	**Upper confidence interval**	**EMM group**
Alpine	Control	0.06	0.16	0.04	0.08	bc
	Reduced biomass	0.07	0.08	0.06	0.08	c
Alpine transition	Control	0.05	0.10	0.04	0.06	b
	Reduced biomass	0.20	0.10	0.17	0.23	d
Subalpine	Control	0.03	0.08	0.02	0.03	a
	Reduced biomass	0.16	0.10	0.13	0.19	d

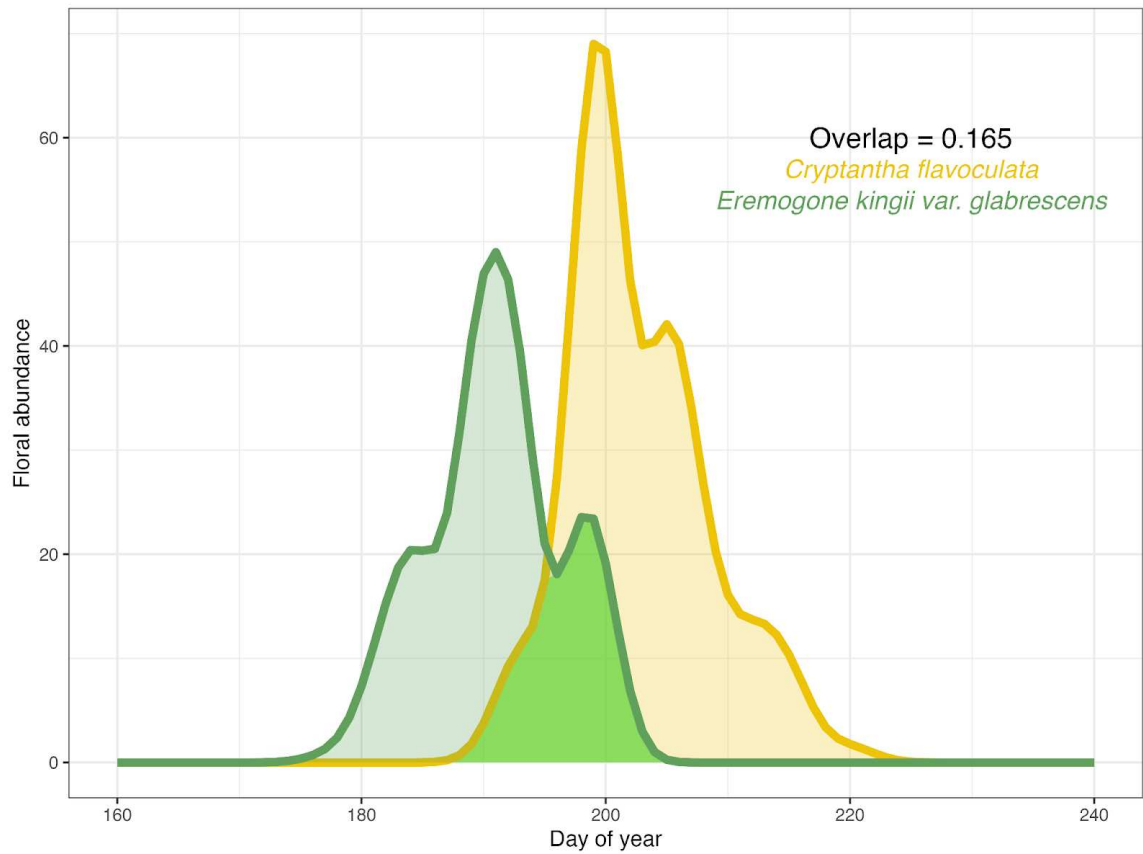Figure 3.1: Satellite image of the subalpine site. Each site contains 2-3 pairs plots.

Figure 3.2: Example of how we calculate phenological synchrony in this study. In green is a phenological distribution of a single *Eremogene kingii var. glabrescens* plant and in yellow is a phenological distribution of an individual *Cryptantha flavoculata* plant at site 1, plot M1 in 2019. The highlighted green area is shared by both individuals. Synchrony is calculated by summing the distributions of both species, and dividing by the shared area. For this example, 16.5% of the shared phenological distribution overlaps.
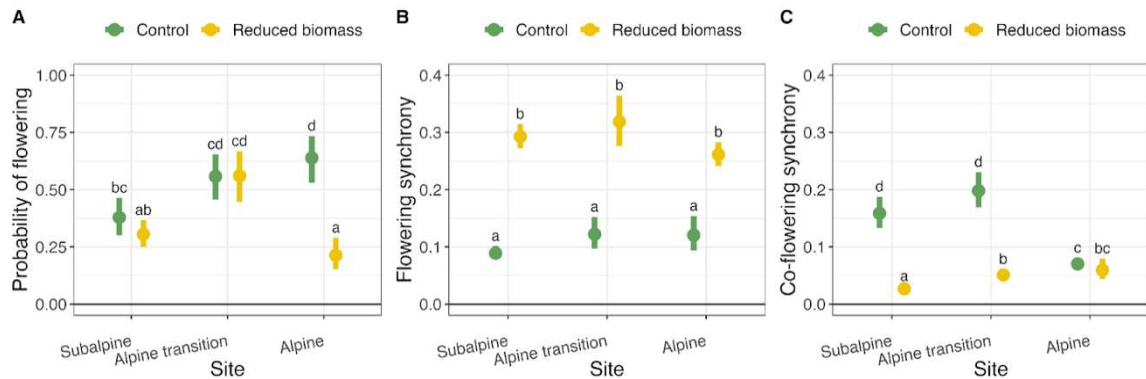
Figure 3.3: Comparing post-manipulation metrics between sites and treatment for A) probability of flowering, B) flowering synchrony, and C) co-flowering synchrony. Points indicate means and error bars indicate 95% confidence intervals. Non-overlapping letters above confidence intervals indicate a significant difference (P < 0.05) between sites and treatments.

Synthesis

Climate change and aridification in dryland ecosystems is altering the co-occurrence and phenological synchrony of plants and pollinators, with the potential to cause a breakdown of these critical mutualistic interactions. Using a 2230 m elevational gradient, we found that more arid conditions will decrease plant-pollinator temporal co-occurrence at the community level, resulting in fewer plants and pollinators potentially interacting (Chapter 1). Further, more arid conditions will decrease plant-pollinator phenological synchrony, meaning the subset of plants and pollinators that do co-occur will be less likely to interact. When breaking down communities into distinct plant taxa and pollinator guilds based on flower visitation, certain groups of plants and pollinators will be better suited to maintain interaction potential with increasing aridity. Using a 14-year time series, we found that phenological synchrony is predicted to decrease for plant taxa and bee guilds that are phenologically active during the summer monsoon season, but not those who are only active during the spring (Chapter 2). The diet breadth of bee pollinators will play an important role in meditating phenological synchrony in more arid conditions, with more generalist floral visitors having a higher likelihood of maintaining phenological synchrony. How plant species respond to increased aridity and drought-induced changes in community composition could help alleviate the negative effects of climate change in dryland ecosystems. We experimentally reduced plant biomass and found that floral phenology shifted in a way that increased conspecific flowering synchrony and reduced or maintained heterospecific co-flowering synchrony (Chapter 3). However, reduced floral abundance in both control and reduced biomass plots could have

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cascading impacts on pollinator abundance, threatening plant-pollinator interactions.

Together, these results indicate that plant-pollinator mutualisms are at risk in dryland

ecosystems due to decreased interaction potential. This dissertation provides some of the

first evidence of these trends and advances our understanding of plant-pollinator

dynamics in an increasingly arid world.