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Phenological Activities of Desert Bees Track Rainfall More Than Temperature and Predict Temporal Abundance Trends Over 16 Years

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PENOLOGICAL ACTIVITIES OF DESERT BEES TRACK RAINFALL MORE THAN TEMPERATURE AND PREDICT TEMPORAL ABUNDANCE TRENDS OVER 16 YEARS

by

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THESIS

Submitted in Partial Fulfillment of the
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DEDICATION

For my grandmother and grandfather, who sparked my curiosity in science by exposing me to the beauties and wonders of nature.

For my mother, whose nature and nurture continue to motivate, support, and inspire me every day.

For my friends Sam and Venu, whose love and support has proven boundless.

For my dog Tiberius, who taught me the depth of connection shared among all life.

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ABSTRACT

Phenology, the timing of recurrent biological events, is a key mechanism by which species adapt or acclimatize to variable environmental conditions, including those influenced by climate change. Measurable traits, including the onset and end of activity, peak activity, and duration, characterize the phenology of life events, and could be significant predictors of trends in population abundance or stability in a changing climate. Bees provide critical pollination services, and understanding the covariates of bee phenological traits can refine predictions on the vulnerabilities of bees and their services to climate change. We paired 16 years of monthly bee survey data (2002-2019) with climate data for 74 bee species in dryland ecosystems of central New Mexico, USA. Contrary to the current paradigm of temperature as the key driver of insect phenology, twice as many bee species had phenological sensitivity to precipitation (39%) than to temperature (20%). Among phenological traits, the end date of active flying periods was most sensitive to climate. Of the 20% of bee species for which precipitation predicted activity end date, 73% ended activity later in wetter years. Fifteen bee species (~20%) had phenological traits sensitive to temperature, but temperature sensitivity was idiosyncratic, and only four species had earlier onset in warmer years, as expected from results in other biomes. Oligolectic (diet specialist) bee species began, peaked, and ended activity later in the year than polylectic (generalist) species, but phenological traits did not correlate with sociality. All phenological traits showed phylogenetic signal, suggesting evolutionary conservatism of phenology among the common bees of central New Mexico drylands. Finally, species with long activity durations were more common, had greater temporal stability in abundance from year to year, and were less likely to decline over time, perhaps because of their longer window for resource acquisition. Our results suggest that drier climates of the future may shift bee phenological activities toward earlier onset, peak, and end dates, that bees with short activity durations may be among the most sensitive to declines in future climates, and that both generalist and social bees may be able to resist or recover from climate change if they have long durations of flight activity.

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INTRODUCTION

Phenology, a life-history trait representing the timing of recurrent biological events, is a key mechanism by which species adapt or acclimatize to variable environmental conditions, including those influenced by climate change (Zettlemoyer and DeMarche 2022). Recent advances in methods for phenological data acquisition (Primack et al. 2023) have led to major improvements in understanding the drivers of phenology (Bellard et al. 2012; Lü et al. 2023), but phenological responses to climate change are still poorly understood for many species (Piao et al. 2019). In particular, data on climate-phenology linkages across diverse taxa within a single ecosystem are rare yet important for understanding the synchronicity of species' responses to climate across a community. For example, 45 years of phenological data for plants, insects, birds, mammals, and an amphibian in a mountain ecosystem revealed significant variation in climate-phenology linkages across taxa, indicative of potential asynchrony in species’ phenological responses to climate (Prather et al. 2023). Phenological cues often differ among taxa; therefore, climate change could disrupt species interactions as phenological cues are altered. For instance, in eastern North America, deciduous trees and wildflowers advanced their leaf-out phenology at different rates under climate warming, which increased canopy shade for early spring wildflowers (Miller et al. 2022). Such asynchrony could also mismatch trophic interactions or interspecific mutualisms (Simmonds et al. 2020). For example, bird species that advanced their laying dates at a slower rate exhibited negative population trends, suggesting these species are becoming mismatched phenologically with their food resources (Franks et al. 2018).
An organism’s phenology is defined by traits that enable adjustment to the environment and could predict trends in population abundance and interannual stability (Hallmark et al., in press). Key phenological traits include onset, day-of-the year a species' presence is first recorded, end, day-of-the year a species is last recorded; and peak, the estimated day-of-year of a species' highest abundance. Phenological duration is calculated by subtracting the onset from the end to estimate the number of days a species is continuously present on the landscape. Phenological traits, like onset, peak,

end, and duration, can change with changing climate, providing acclimatization potential to survive environmental change or causing rapid population declines when phenological mismatches to climate occur (Dorian, McCarthy, and Crone 2023). Specific climate predictors of phenology include snowmelt timing; earlier snowmelt reduces overlap in flowering for co-occurring wildflowers, which could, in turn, reduce plant competition for pollinators under climate warming (J. Forrest, Inouye, and Thomson 2010). Water availability can also be a potent driver of phenology; for example, seasonal drought predicted tree flowering in a Bornean rainforest (Brearley et al. 2007).

Despite the potential importance of phenological traits to the fitness of organisms faced with shifting environmental conditions, relatively few studies have evaluated phenology as a predictor of long-term trends in population abundance or of which species are winning vs. losing (increasing or decreasing) over time (Zettlemoyer and DeMarche 2022). Phenological traits may also help to explain differences among species in the temporal stability of population abundance, particularly those facing environmental change. In plants, non-phenological traits were highly predictive of long-term stability in plant population abundance (Májeková et al. 2014). Changes in population stability can alter niche partitioning by shifting phenological overlap among species within the same guild, potentially eliminating species interactions or creating new ones (Ma et al. 2021). The exploration of bee phenological traits as correlates of abundance trends and stability may help to refine predictions on bee species declines, particularly for understudied but ecologically important native bees (Willmer, Cunnold, and Ballantyne 2017; Garibaldi et al. 2013). Surprisingly, few studies have implicated phenological traits in temporal population stability (see Hallmark et al. in press), yet such investigations could increase understanding of species' vulnerabilities to climate disruption.

Covariation between phenological traits and other well-documented life history traits could speed efforts to predict species' acclimatization potential to climate via short-term phenological change. For example, easy-to-measure life history traits could strongly predict harder-to-measure phenological traits, thereby sharpening our estimates of species' sensitivities to environmental change. For instance, in the bee genus Osmia, phenology covaried with diet specialization: species with earlier phenologies were more often dietary generalists than specialists, indicating that a generalist strategy may be favored during early spring when the composition of flowering plant species is least predictable (Pelletier and Forrest 2023). However, diet specialist bees outperformed generalists in a desert bee community under drought due to phenological synchrony with the blooming of their host plant, creosote bush (Larrea tridentata; R. L. Minckley, Cane, and Kervin 2000). However, such covariation is poorly resolved for most taxa, highlighting the need for an increased understanding of relationships between phenological and life history traits (Colom et al. 2022; Stemkovski et al. 2023).

For arthropods, temperature has been the primary axis of investigation among climate drivers of phenology (Colinet et al. 2015; J. R. Forrest 2016; Musolin 2007; Vasseur et al. 2014). Across a subset of North American bee species, phenology has advanced by an average of 10.4 days during the past 130 years, primarily since 1970, in concert with global warming (Bartomeus et al. 2011). These shifts in bee emergence matched the timing of flowering host plants, the advancement of which paralleled global temperature increases (Bartomeus et al. 2011). However, despite the historical focus on temperature, arthropod phenologies may be more closely coupled to water availability in some ecosystems where water is a limiting resource due to water costs of gas exchange and the limitations in adaptability to water stress from both the plant and pollinator perspective (Gérard et al. 2020; Chown, Sørensen, and Terblanche 2011). Indeed, bee phenology in a dryland system may be more closely coupled to water than for other arthropods because flowering plant phenology is well documented to respond to water availability (Castillioni et al. 2022), and coevolutionary dynamics between flowering plants and bees allow many species to track floral availability and abundance (Almeida-Neto, Prado, and Lewinsohn 2011). In one study, bee community composition varied with drought, indicating that bees responded to local precipitation with diapause cues tied to host plant activation by rain events (Minckley, Roulston, and Williams 2013). In diverse communities of bees, species likely vary in which phenological traits track which aspects of climate, highlighting the importance of considering precipitation in addition to temperature as a direct or indirect driver of phenology, which few studies have done.

We analyzed 18 years of monthly pan trap data representing native bee activity (2002-2019) to evaluate the sensitivity of bee phenology to climate variables, the importance of phenological traits as predictors of temporal trends and stability in abundance, and the covariation between phenological traits and other life history traits. To address the following questions, we quantified the phenological traits of 74 abundant bee species across three dryland ecosystem types in central New Mexico, USA. (1) How sensitive are bee phenological traits to temperature versus precipitation? We predicted that bee species would be more phenologically sensitive to precipitation in drylands, in contrast to the current paradigm that has emphasized temperature sensitivity for arthropods. (2) Do phenological traits predict which bee species have temporal stability in abundance, their commonness or rarity, or if their abundances have increased or decreased over time? We hypothesized that species with long phenological durations would have low temporal stability and be most likely to decline over time because they experience extended exposure to acute weather events such as drought, extreme heat or severe storms. Alternatively, a long phenological duration may provide a prolonged window for resource acquisition, buffering population abundance against resource shortages that occur in short time frames due to climate extremes, thereby increasing stability and reducing the likelihood of population declines. We also expected bee species with early onset dates to have less stable population abundance than species emerging later in the year because of unpredictable spring rains and correspondingly high variability in the phenology of early-blooming plants (Kimball et al. 2011). In contrast, bees with late-onset should have greater temporal stability because of more consistent water availability and floral abundance during the summer monsoon rainy season (Sponseller et al. 2012). Lastly, we asked (3) Do phenological traits covary with other life-history traits or evolutionary history? We expected that social bees would have longer phenological durations than solitary bees because of the time required to establish colonies and the buffering capacity of colony formation (Kocher et al. 2014). We additionally evaluated diet breadth as a correlate of phenological traits for solitary bees, excluding focal social bees who were all generalists. We predicted that oligolectic (floral specialist) bees would have shorter activity durations because their foraging window is constrained to the blooming of one or a few plant species (Minckley, Roulston, and Williams 2013). We also evaluated whether bee phenological traits mapped onto the bee species phylogeny, indicative of phylogenetic conservatism of phenological traits, which would make it easier to predict the phenologies of unstudied taxa and the potential for phylogenetic ‘constraints’ on phenological plasticity.

METHODS

Study Locations

To examine the drivers and impacts of bee phenology, we used data collected as part of the Sevilleta Long Term Ecological Research program (LTER) at the Sevilleta National Wildlife Refuge (SNWR) in Socorro, New Mexico, USA. Central New Mexico supports more than 300 native bee species (Kazenel et al. 2020), making it an ideal location to examine the phenological dynamics of diverse native bee communities Minckley and Radke 2021; Orr et al. 2021). The SNWR spans multiple ecosystem types, including the three in which we conducted our study: Chihuahuan Desert shrubland, dominated by long-lived creosote bush (Larrea tridentata) (34.3329, -106.7358), Chihuahuan Desert grassland, dominated by black grama grass (Bouteloua eriopoda) (34.3362, -106.7212), and Plains grassland, dominated by blue grama grass (B. gracilis) (34.3364,-106.7212) (M. R. Kazenel et al. 2020). The desert grassland and desert shrubland sites are separated by ~2 km and share a meteorological station, while the plains grassland is ~10 km from both desert sites, with a separate meteorological station that collects hourly data, including rainfall and air temperature. We summarized yearly values for annual precipitation and average air temperature at each station for climate analyses (Moore and Hall 2023).

Future state transitions among these ecosystems are predicted under climate change, with Desert shrubland replacing Desert grassland and Desert grassland replacing Plains grassland (Zinnert et al. 2021). All ecosystems have a diverse flora, comprised of both annual and perennial forbs and grasses, with some shrubs and sub-shrubs (Baker et al. 2019), and are protected from many common anthropogenic disturbances, e.g., pesticide use, cattle grazing, and traffic. Non-native European honeybees (Apis mellifera) are largely absent from study sites. In the region, monsoon season aridity and interannual variability in aridity have increased over the past 100 years (Rudgers et al. 2018; Maurer et al. 2020).

Bee Surveys

In our study region, bee activity and flowering occur primarily between spring rains (March-May) and cold weather post-summer monsoon (October-November). There is a lull in plant activity during peak summer temperatures (July-August) until monsoon rains begin (Muldavin et al. 2008). Bee sampling is ongoing and occurs monthly from March to October. Each month, traps are opened for 14 days, usually beginning on the first day of spring. Bees are collected, rinsed, and stored in 70% ethanol at the end of each 14-day trapping period. Traps are then closed for the next 14 days, with this cycle continuing through October.

Bees are collected in a ‘Buchmann Funnel Traps’, which are a form of passive bee trap that sits at both the north and south ends of five 200-m transects in each of the three ecosystem types. Each trap consists of a painted funnel (height = 10 cm, top diameter = 14 cm, bottom diameter = 2.5 cm) atop a 946 mL paint can filled with ~275 mL of propylene glycol (M. R. Kazenel et al. 2020). Funnels were randomly assigned to be painted either fluorescent blue or yellow, with one trap of each color per transect and ten traps per ecosystem type, comprising 30 traps in total. Traps were surrounded by chicken wire and placed on a platform ~45 cm above the ground for protection from wildlife disturbances and weather. Passive sampling methods like funnel traps, similar to pan traps, can reduce collector sampling bias (Westphal et al. 2008) but are known to have other biases, including taxonomic bias against social bees and the potential for abundance bias in relation to floral resource availability (Montgomery et al. 2021; Baum and Wallen 2011). The results of this sampling are presence counts of bee species with an attraction for passive funnel traps. However, trapping methods do not bias the results within this study because the same survey methods were used across years and climate contexts.

Our research focused on monthly resolutions of adult bee flight periods that result primarily from direct temperature and moisture effects on the physiology and development time of all life stages; eggs, larvae and pupal emergence, but are beyond the scope of this study. Two incomplete sampling years (2016, 2017) were removed from the dataset before analyses. Then, the bee count data from the traps were grouped and summed by month, year, and focal species (see below) using ‘ddply’ in the ‘plyr’ package (Wickham 2011). Bee species frequency was calculated based on the total number of years a species occurred over the entirety of the dataset. Bee species that occurred during five or fewer years were removed, leaving 74 focal bee species in the dataset. All bee count data are publicly available (Wright et al. 2023).

Bee Identification and Life History

Bees were identified to species with additional information added by bee specialists and co-authors Dr. Karen Wright and Dr. Terry Griswold. Diet breadth and sociality data were aggregated from the literature (Bryan N. Danforth et al. 2019; M. Kazenel 2023), and by the above-mentioned experts. Bee diet breadth information varied among sources but was consistent enough to categorize all 74 species as polylactic (generalists) bees, who visit a wide range of plant species, and oligolectic(specialists) bees who rely on a limited number of plants or even a single plant species, or cleptoparasitic for bees that parasitize other bees. Social structure categories varied from solitary, often referring to a single bee foraging, provisioning, and laying the egg for their nest, to social, bees that tend to have a division of labor between casts, and also included communal bees with aggregate nesting but solitary foraging behviors. 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 on specimens is available via the Symbiota Collections of Arthropods Network (SCAN. 2019).

Focal Bee Species

We conducted our analyses on 74 focal bee species. We focused on common species (observed in >5 years during 2002-2019) because the inclusion of rare species could lead to biased or highly uncertain estimates of phenological traits due to inconsistency in their activity periods and low sample sizes. Focal species represented

92% of total bee abundance in the entire bee monitoring dataset (Supplementary Material, Appendix 1). Five of the six bee families recorded at the SNWR were represented in the focal dataset; the only family not included was Melittidae, which represented only 2 of the 341 species observed. For 6 of the 8 sociality and diet breadth categories, grouped by species count (Supplementary Material, Appendix 1), the focal species set represented 20% or more of the total species comprising any given category at the SNWR. For example, the focal species set accounted for 53% of polylectic bees, 23% of oligolectic bees, 32% of solitary bees, and 25% of social bees.

Potential Research Biases

Most studies' results and conclusions are confined by methodology biases. Since our study employed passive funnel traps for bee abundance, data collection may be susceptible to various biases that can impact the reliability and generalizability of the findings (Montgomery et al. 2021). One potential source of bias lies in trap placement, as the traps' effectiveness in capturing bees can vary based on the specific location within the study area. Factors such as floral abundance, microhabitat characteristics, and proximity to nesting sites may influence the capture rates, potentially skewing the representation of bee species. Additionally, the temporal bias could arise if traps are deployed during specific seasons or times of the day, overlooking variations in bee activity patterns. Trap attractiveness and selectivity for certain bee species might introduce another form of bias, as some species may be more prone to enter the traps than others, leading to an underrepresentation of certain taxa. Focal species selection has limitations due to the reduced sample size of 74 species. Variation only present in the bees that can refrain from activity in substandard years may not be captured. Lastly, the bias may emerge from the trap design itself, favoring certain bee sizes or morphologies, which could result in an incomplete picture of the overall bee community structure. Acknowledging and addressing these potential biases is crucial for enhancing the robustness and validity of this study's conclusions regarding adult bee abundance activity.

Bee Phenological Traits

For the 74 focal species, we calculated the phenological traits of onset, peak, end, and duration (Table 1). Traits were determined for each year of bee observation for each species and averaged for each species over the full-time series. A circular distribution function was used to calculate phenological traits so that traits were not constrained by a 1-to-12-month calendar year (Staggemeier et al. 2020). Briefly, onset was determined as the day of year when 5% of the species' total yearly abundance was observed and end was when 95% had been observed. To obtain these estimates, first, bee abundances were converted into 0/1 presence-absence observations. The day in the middle each month was used to represent whether bees are present or absent. Day of year (DOY) was converted to radians for each abundance observation to be used in circular statistics. The ‘densityFit’ function (bandwidth = 20) fit a circular density distribution to the transformed data, using the von Mises distribution, a circular analogue of the normal distribution, which provided a daily resolution metric based on our monthly presence absence data (Ridout and Linkie 2009). The resulting bee abundance values in the circular distribution were rounded to 0.001. The peak day of the circular distribution was determined as the day of the year with the highest abundance density. Furthermore, the days preceding and following the peak were separated respectively. The onset and end dates were determined by filtering `before.peak` and `after.peak` bee abundance values, based on a specified threshold (0.05 in this case), and then cataloged as the corresponding `DOY` values. Estimated metrics of general onset, peak, and end were calculated for each of the 74 focal bee species in each year. The duration trait was calculated by subtracting the onset date from the end of activity date. Among the 74 bee species, 5 had phenological activities that included a pause between onset and duration, typically lasting 1 month (i.e., 1 trap period), during which the species had zero abundance. Because our analyses used yearly climate data, rather than monthly, we did not adjust duration for years in which one or more months between onset and end had zero observations. Future analyses to link phenology with shorter climate windows would be the best format to investigate such pauses.

Statistical Analysis Methods

(1.) How sensitive are bee phenological traits to temperature versus precipitation?

We fit linear regression models of the form: phenological trait ~ climate variable, to evaluate the relative importance of annual temperature and annual precipitation as predictors of each bee species' yearly phenological traits, leveraging the large interannual variability in climate during the 16-year time series (n = 16 observations per model). Models used the `lm()` function in base R (R Core Team 2023). Climate variables were standardized to mean = 0 and standard deviation = 1 to compare the relative magnitudes of slopes between temperature and precipitation, which are measured in different units. We evaluated each of the phenological traits of onset, peak, end (units are day of year), or duration (units are number of days) separately. Analyses used the `fit_model` function and the `map()` function from the `purrr` package (Wickham, Henry, and RStudio 2023). For the bee taxa with climate-sensitive phenologies ($P < 0.1$), we visualized the sensitivity of phenological traits to climate in package 'ggplot2' (Wickham 2016) with points colored by the family of the bee species and the size of the points indicative of the level of statistical significance of the climate sensitivity.

(2.) Do phenological traits predict which bee species have been winners or losers over time, their commonness or rarity, or their temporal stability in abundance?

Temporal trends, commonness-rarity, and stability. For each focal bee species in each ecosystem type, we determined the temporal trend as the slope of change in bee abundance over time (positive slope=winner species, negative slope=loser species) and its standard error as a measure of uncertainty in temporal change. For each ecosystem type, we also determined each species' commonness-rarity as the maximum abundance over the time series, with 'common' bees consistently having a higher relative maximum abundance. Maximum abundance was used to avoid biases related to the number of months a species was collected and their cumulative abundance. This avoids the potential sampling artifact associated with longer durations equating to higher mean annual. We calculated the temporal stability in abundance as 1/CV of abundance over time (Wisnoski et al. 2023).

Model construction and assumptions. We related each phenological trait (onset, peak, end, or duration) to temporal trend, mean abundance, and temporal stability across the set of 74 focal bee species using mixed effects linear regression models that included the random effect of species identity to account for individual species that occurred in more than one ecosystem type. Models were fit with maximum likelihood estimation using the ‘lmer’ function in package ‘lme4’ (Bates et al. 2015). To evaluate temporal trends in abundance, we weighted each slope value by 1/SE of the slope, in order to downweight trends with high uncertainty. In addition, trends that did not differ from no change (zero slope) at $P < 0.1$ were set to slope = zero. Using all trend estimates rather than setting the slope to zero or using unweighted models returned qualitatively similar but less conservative results, so we presented results from the most conservative approach. For commonness-rarity, we log-transformed maximum bee abundance to meet model assumptions of normality of residuals and homogeneity of variances. Still, the other two metrics required no transformation to meet model assumptions.

Ecosystem differences. We compared the models described above against models that included the ecosystem and its interactions with phenological traits to consider whether trait-abundance relationships varied among ecosystem types. We report results from ecosystem-dependent models only for commonness-rarity because they fit the data better than simple models for which phenological traits predicted abundance evenly across the three ecosystem types. Commonness-rarity was ecosystem-dependent for onset (delta AICc = 10.2) and duration (delta AICc = 13.2). In these cases, we tested for differences among ecosystems in mean phenological traits using function pairs (‘emtrends’) from the ‘emmeans’ package for mixed effects models (Lenth 2018).

(3.) Do phenological traits covary with life history characteristics or track evolutionary history?

Life history trait covariation. Across the focal 74 bee species, we tested for relationships between phenological traits (onset, peak, end, or duration) and two bee life history traits: diet breadth, which included levels of oligolectic, polylectic, or cleptoparasitic, and sociality, which included levels of communal, parasitic, social, and solitary. Communal bees are solitary bees that use a single entrance to the nesting site, but each bee digs its own nest from that point; among the 74 bees, 2 Agapostemon species were communal.

We used general linear mixed-effects models of mean phenological trait as a function of each life history trait x ecosystem type. The interaction accounted for the possibility that trait covariance differed among ecosystems (e.g., due to differences in climate, plant phenology, or resource availability). Bee species identity was included as a random effect to account for replicated observations of the same species across the three ecosystems. Models were fit with maximum likelihood estimation using 'lmer' in package 'lme4' (Bates et al. 2015), as described in question 2. If interactions with ecosystem type were significant (which occurred only for end ~ sociality, delta AICc = 1.7), we tested for differences among ecosystems in mean phenological traits across life history traits using function 'pairs' from the 'emmeans' package (Lenth 2018). However, in all cases, because the relationships were consistent in direction (just not magnitude) among ecosystem types, our visualizations combined across ecosystem types.

Bee phylogeny. To construct a phylogeny, we used genus-level tree data from Hedtke et al. (2013), which we pruned to include only the genera in our dataset (Paradis and Schliep 2019a). We added species as polytomies (Pearse et al. 2015; Paradis and Schliep 2019a) because species relationships are unresolved within many genera (Danforth et al. 2019).

Phylogenetic signal. We tested for phylogenetic signal in bee phenological traits (onset, peak, end, and duration) using the R package 'phyloSignal', which enabled the calculation of Moran's I index (Gittleman and Kot 1990), Abouheif's C mean index (Pavoine et al. 2008), Blomberg’s K and K* (Blomberg, Garland JR., and Ives 2003) (Blomberg et al. 2003), and Pagel’s lambda (Pagel 1999). For each index, we tested the null hypothesis that phenological trait values were randomly distributed across the phylogeny, except for Pagel’s lambda, which was evaluated with a likelihood ratio test (Keck et al. 2016). We used the ‘ggtree’ package to visualize the correspondence of phenological traits with bee phylogeny (Yu 2022).

Phylogenetically independent contrasts. For questions 2 and 3, we considered relationships with phenological traits using phylogenetic independent contrasts (PICs) as our units of replication, rather than the populations of each species. Here, we included polytomies for species populations as tips on the phylogeny in cases where species occurred in more than one ecosystem type. For question 2, we evaluated relationships between phenological traits and bee abundance metrics to account for evolutionary history using regressions of phylogenetically independent contrasts (PICs) (Garland, Harvey, and Ives 1992). We conducted PIC analysis using R package ‘phytools’ and function ‘pgls.SEy’ quantitative traits (Ives, Midford, and Garland 2007; Revell 2012), but alternative methods using the package ‘ape’ with function ‘gls/corPagel’, (Paradis and Schliep 2019b)returned nearly identical results. To evaluate differences among phenological traits for the categorical traits of sociality and diet breadth with phylogenetic correction (question 3), we used simulation-based phylogenetic ANOVA (Garland et al. 1993) with function ‘phlyANOVA’ in package ’phytools’ (Revell 2012) with 1000 simulations.

RESULTS

Bee Phenological Trait Diversity

The focal bee community represented substantial interspecific and intraspecific variation in bee phenological traits (Fig. 1-2). Across the 74 focal bee species (Table S1), phenophase durations ranged from 70 days, recorded for Megachile policaris, to 212 days, recorded for Lasioglossum semicaeruleum. The earliest onset was 45.25 ± 0.1 s.e. DOY (~15 February) for Anthophora porterae and the latest was Melissodes snowii with 232 ± 5.3 s.e DOY (~20 August). Across the focal bee community, there were two main peaks in onset, one for spring-active species and one during the summer-fall monsoon. The earliest end date was 119.58 ± 2.3 s.e DOY (~29 April), recorded for Anthophora porterae, while the latest end date was 309.64 ± 4.83 s.e (~5 November), recorded for Melissodes snowii. The date of peak abundance varied considerably among bee species, from March to September, with a difference of 191 days between the species with the earliest peak and that with the latest peak (a subset of species are shown in Fig. 2). Year to year variability of duration also differed among species. For example, Eucera lycii had the least variability over 16 years with duration ranging from 1-2 months, while Halictus ligatus durations ranged from 2-7 months. Species' peak of activities shifted from year to year, possibly in concert with the indirect effects of climate on plant resource availability (Ogilvie et al. 2017).

(1.) How sensitive are bee phenological traits to temperature versus precipitation?

Consistent with our hypothesis, almost twice as many bee species had phenological sensitivity to precipitation (39%) relative to temperature (20%) (Figs. 3-5, Table S2). Among the phenological traits, the end date of flight activity was the most sensitive to climate variables (Fig. 3C), with 20% of species sensitive to precipitation and 7% of species sensitive to temperature.

Precipitation sensitivity. Of the 74 bee species, 29 (39%) had phenological traits that were sensitive to annual precipitation at $p < 0.1$ (Fig. 3, Table S2, Fig. S2). Eight of the 29 species had phenological sensitivity to annual precipitation for more than one phenological attribute.

Onset was sensitive to precipitation for 14% of species (Fig. 3A). Bees generally had a later onset in wetter years (10 species), although onset was earlier in wet years for one outlier species, Megachile policaris. This advancement of onset with more precipitation was particularly strong in Lassioglossum species 7 (slope, $\beta > 25$ days earlier per 1 s.d. increase in annual precipitation), while Diadasia ochracea had the most significant response ($p < 0.01$).

Peak activity occurred later in wet years for six species; however, for two species, Melissodes agilis and Megachile policaris, peak activity occurred earlier in wetter years. The relationship between peak and precipitation was particularly strong ($\beta \sim 25$ days) in Lassioglossum semicaeruleum and Halictus tripartitus (both members of the Halictidae family). Again, like onset, Diadasia ochracea had the most significant advancement response ($p < 0.01$).

The end date of activity was the phenological trait most sensitive to precipitation, with 20% of species having an end date that was sensitive (Fig. 3C). Of the bees with precipitation-sensitive end dates, 73% ended activity later in wetter years. This shift was strongest ($\beta > 25$) for Sphecodes species 1, Sphecodes species 6, Lasioglossum morrili, and Halictus tripartitus (all Halictidae). The most significant responses (all $p < 0.01$) were shared among Sphecodes 6, Halictus tripartitus, Dioxys pomonae, and Anthophora affabilis.

Species’ duration of flight activity either shortened or lengthened in response to mean annual precipitation, with 18% of species sensitive to precipitation. Of those, the majority (58%) had shorter durations in years with more rain. Halictus tripartitus had the longest extension of activity ($\beta > 25$ days longer per 1 s.d. increase in annual precipitation) and the most significant response ($p < 0.01$), while Sphecodes 4 and Melissodes agilis had the most shortened durations in response to precipitation.

Temperature sensitivity. As predicted for this dryland bee community, temperature did not correspond with nearly as many species' phenological traits as precipitation. Of the 15 bee species with phenologies sensitive to temperature, only seven species tracked temperature across more than one phenological trait.Only one species, *Habropoda morrisoni,* was phenologically sensitive to temperature for onset, peak, and duration, but not end of activity.

Across the 15 temperature-sensitive bee species, duration was the phenological trait most sensitive to temperature, but patterns were idiosyncratic (Fig. 4). Of the 10 species with temperature-sensitive durations (13.5% of total bee species), 30% had shortened durations and 70% had lengthened durations with warmer mean annual temperature (Fig. 4, Table S2). Three species, *Megachile lobatifrons, Macrotera latior,* and *Lasioglossum sisymbrii*, had shortened durations during warmer years, while the seven bee species that had elongated durations in warmer years included members of families Apidae, Megachilidae, Andrenidae, and Halictidae.

All of the bee species with onset sensitive to temperature at $p < 0.1$ (5% of total bees we evaluated) had later onset in years with warmer mean annual temperature (Fig. S1A, Table S2). *Lasioglossum* species 7 had the strongest shift ($\beta = -38$ days per 1 *s.d.* increase in MAT) and the most significant shift ($p < 0.01$) while *Habropoda morrisoni* had the weakest shift ($\beta = -9.2$ days per 1 *s.d.* increase in MAT).

For peak activity date, 5% of focal bees were sensitive to temperature (Fig. S1B, Table S2). Only one species, *Dufourea vernalis*, had one of the most significant shifts with a later peak in warmer years ($p < 0.05$); the remaining three species peaked earlier in warmer years. *Habropoda morrisoni* had one of the strongest earlier shifts in peak activity in relation to temperature ($\beta < -30$).

The estimated date for the end of activity was sensitive to temperature for 7% of focal bee species (Fig. S1C, Table S2), but the direction of sensitivity was inconsistent across species. Two species, *Melissodes thelypodii* and *Diadasia megamorpha* (both Megachilidae), had later end dates in warmer years, while three species, *Megachile* *lobatifrons, Lasioglossum sisymbrii,* and *Lasioglossum* species 7, had earlier end dates in warmer years (Fig. S1C, Table S2).

(2.) Do phenological traits predict which bee species have been winners or losers over time, their commonness or rarity, or their temporal stability in abundance?

Duration was the best phenological predictor of temporal stability in bee abundance, bee commonness-rarity, and temporal abundance trends of winners versus losers across the focal desert bees (Fig. 5, Table S3). Bee species with shorter durations were less stable from year to year in abundance, while bees with longer durations of activity, mostly concentrated in the Halictidae family, were more stable (Fig. 5A). This result remained even when accounting for bee evolutionary history using phylogenetically independent contrasts (PIC slope (β) = 0.006 ± 0.001 s.e, $p < 0.01$). Bees with longer durations had higher year to year maximum abundances than bees with short durations based on our metric for commonness (Fig. 5B), with a significant relationship detected between ecosystem types. This result also remained with phylogenetic correction (PIC slope (β) = 0.041 ± 0.004 s.e, $p < 0.00001$). Lastly, bees with longer durations were more likely to have increased in abundance over time, while the bee species in decline had the shortest durations (Fig. 5C, PIC slope (β) = 0.012 ± 0.002 s.e, $p < 0.00001$). Although winner bee species over time were concentrated in the family Halictidae, the few bees that significantly declined over the 16 years were split between the families Halictidae and Apidae (Fig. 5C). A later end date of activity also predicted greater temporal stability in the abundance of communal and social bees (Appendix 2, Fig. S3). However, duration was overall the strongest predictor for all abundance metrics (Table S3).

(3.) Do phenological traits covary with life history characteristics or track evolutionary history?

Life history characteristics. Diet breadth emerged as an important correlate of bee phenological traits. Onset, peak, and end varied significantly with different diet breadth (Fig. 6), although duration did not (Fig. 6A; diet breadth $X2 = 2.03$, $p < 0.4$; phylogenetically corrected $F = 4.27$, $p = 0.308$). Specialist (oligolectic) bees had, on average, 57% later onset (Fig. 6B, diet breadth $X2 = 29.9$, $p < 0.00001$; phylogenetically corrected $F = 34.7$, $p = 0.001$), 39% later peak (Fig. 6C, diet breadth $X2 = 29.3$, $p < 0.00001$; phylogenetically corrected $F = 34.4$, $p = 0.001$), and 25% later end of activity dates (Fig. 6D, diet breadth $X2 = 19.5$, $p < 0.00001$; phylogenetically corrected $F = 24.5$, $p = 0.002$) than cleptoparasitic or polylectic bees. Surprisingly, despite their divergence in diet compositions, cleptoparasitic and polylectic bees had similar phenological patterns (Fig. 6).

Two social groups had significantly longer durations than solitary bees (Fig. S2): Communal bees had 77% longer duration and social bees had 46% longer duration (sociality $X2 = 28.7$, $p < 0.00001$; phylogenetically corrected $F = 20.2$, $p = 0.002$), possibly due to the time needed for brood rearing and colony development. However, duration did not play a pivotal role for the rest of the sociality categories as we detected no significant relationships (Fig. S2).

Phylogenetic signal. All phenological traits consistently had significant phylogenetic signal (Fig. 7) across all tests for signal. Moran’s I, Blomberg’s K,K.star, and Pagel’s lambda, all yielded P-values < 0.05. Some examples of strong phylogenetic signal included the finding that sister clades Peridita and Macrotera both trended towards later phenological widows while Andrena species had earlier phenological windows. The closely related genera of Diadasia, Martinapis, Melissodes, and Svastra all had similarly late phenological widows. However, closely related Eucera did not, which may be a novel adaptation towards early season phenology within the clade. In contrast, all of the species in the genus Osmia trended toward early-season phenological windows. Of the 16 genera with more than one species represented, ten genera shared the same trend among all sister taxa, and 12 genera shared the same trend with the exception of one species. These exceptions could be investigated further and included the onset trait of Melissodes tristis, and the opposite trending phenological window of Anthophora montana.The moderate to strong associations between phylogeny and phenology (Fig. 7) suggest that the evolutionary history of bee species plays a meaningful role in shaping the timing of these important life cycle events, although our 74 focal species represent only a small fraction of the potential species in the bee phylogeny, including many that have yet to be described.

DISCUSSION

Our results demonstrate large phenological variability among common desert bee species, as well as substantial intraspecific year-to-year variability. Here, we ascribed variation in phenological traits among species to their phylogenetic relatedness and life history strategies, particularly diet breadth. In addition, year-to-year variation in phenological traits within bee species was more strongly predicted by precipitation than temperature, a pattern that has been infrequently tested for terrestrial insects. Finally, species with long phenological periods of activity were among the most abundant, the most temporally stable, and the most likely to be increasing in abundance over time (winners) relative to species with short phenological windows of activity.

Bee phenological traits were more sensitive to precipitation than to temperature.

For a set of focal bees in drylands of central New Mexico, phenological traits were almost twice as likely to be sensitive to precipitation as to temperature. In particular, we found shifts towards later seasonality in wetter years among the majority of species that responded to climatic variables. These results support our hypothesis that more dryland bee species track precipitation than temperature, contrary to the current paradigm for terrestrial insects (Musolin 2007; J. R. Forrest 2016). In our dryland system, 20% of species had an end date of activity that was sensitive to precipitation, and 73% of those precipitation-sensitive species shifted activity later in wetter years. These results reinforce the findings from other studies conducted, one on desert bee phenology where bee larval emergence was induced by rainfall (Danforth et al. 1999) and another in a montane system where adult bee emergence was sensitive to seasonal variation in advancing earlier snowmelt timing (Stemkovski et al. 2020). All of which suggests that the strength of precipitation sensitivity versus temperature sensitivity may be system-dependent and understated.

We speculate that our focal species may be adapted to respond to the intensity of monsoon summer rains. This attunement could be vital to bee fitness due to the tight relationship between plant productivity and precipitation (Maurer et al. 2020). Without synchronization to the phenology of flowering plants, bees could miss critical windows of availability for essential floral resources. Even small variations in floral resource pulses can have significant impacts on bee foraging responses (Crone 2013). As variability in monsoonal precipitation events increases, we could see declines in floral resource availability and in turn population abundance; as one study illustrated, when drought effects on floral resources interacted with invasive bee competition it led to declines in native bee populations (Thomson 2016). Our results suggest that an even finer-grained understanding of the relationship between bee phenology and precipitation, such as the influence of monthly precipitation or daily rain event size, may improve the prediction of when bees are most active and abundant for pollination services.

The summer monsoon is a staple of climate in the study region with variability of its own. In years with higher monsoonal precipitation, we tend to see lower non-monsoonal precipitation and vice versa. If dryland bee phenology responds more strongly to precipitation than temperature, species may be able to withstand, through adjustments of phenology, the increasing variability in the frequency and magnitude of rain events in the southwestern US (Petrie et al. 2014; Fust and Schlecht 2022; Terry, O'Sullivan, and Rossberg 2022). For instance, solitary bee species typically construct their nests in the ground, in cavities, or in dead plant material (Bryan N. Danforth et al. 2019), and the timing and effectiveness of nesting activities can be influenced by factors such as soil moisture or plant phenology. Increasing soil moisture, such as run-off during a large rain event, can have devastating effects on ground-nesting bees and associated fauna (Fellendorf, Mohra, and Paxton 2004). Therefore, dryland bee responsiveness to precipitation may allow for shifts in phenological timing that enable bees to avoid nesting during undesirable soil moisture conditions. Future work could deepen this investigation by monitoring soil moisture and the nest status of bees or examining shorter time windows of precipitation as predictors of bee phenological activities.

Is bee seasonality lagged due to holding out for monsoon rains when springs are dry? If so, our findings predict that as climate aridifies in the southwestern US, many bee species may shift to earlier seasonality, including earlier onset, peak, and end of activity, which could expose bees to more extreme weather events. Bee species in our system rely on overwintering diapause to survive through the cold months. Climate can influence the timing and duration of overwintering periods and can affect the weight of individual bees (Fründ, Zieger, and Tscharntke 2013). If our focal bees are more sensitive to precipitation than temperature, most likely driven by monsoonal rains, then we may also expect variability in other life stages including their overwintering durations, emergence timing, and body size in seasons following forecasts of increasingly drier years into the future (Williams, Cook, and Smerdon 2022; Munson et al. 2022; Gutzler 2013; Gutzler and Robbins 2011).

An important conclusion is acknowledging the 34 focal species that did not have phenologies sensitive to mean annual climate metrics. These may be the species that remain dormant in years with inclement weather. One study shows that diapause in a solitary bee species Megachile rotundata was highly influenced by their thermal history (Yocum et al. 2006). Rather than shifting their phenologies in response to atypical seasonality they instead remain in diapause until climate conditions are ideal. This would be an exciting direction for future research since diapause has been linked to survival and colony development in social bees (Gosterit and Gurel 2009) but seems to be understudied in solitary bee.

Longer duration of activity best predicted winners over time, bee commonness, and the temporal stability of bee abundance.

Duration was the best predictor of all bee abundance metrics among the phenological traits we examined. Species with longer durations were more likely to increase over the past 16 years, were more stable in abundance during that time period, and were more abundant on average than species with short activity periods. These results supported our hypothesis that a lengthy window of phenological activity can offer an extended opportunity for resource acquisition, acting as a safeguard against resource shortages during shorter time frames. This safeguard, in turn, appears to enhance stability and decrease the probability of population decline. Longer durations have been associated with increases in relative abundance in another group of arthropods, butterflies (Michielini, Dopman, and Crone 2021). Similar investigations could be useful for other terrestrial invertebrate taxa to determine whether this pattern is generalizable.

We theorize that bees that are active for a longer period each year can take advantage of a wider range of floral resources. This wide window of opportunity may be particularly important when floral resources are seasonal, limited, or highly variable in response to climate (Park 2016; Craine, Wolkovich, and Towne 2012). A longer phenological duration could give bees greater opportunity to adjust their foraging behaviors and capitalize on resource availability, in turn buffering their populations against temporal changes in floral distribution. One study observed that bumble bee abundances were driven by the indirect effects of climate via the temporal distribution of floral resources (Ogilvie et al. 2017). Coincident with this hypothesis, the pattern that winners over time had longer phenological durations was strongest for generalist (polylectic) bees (Fig. S2), which can adjust their diets more readily than specialists on the temporally available plant species or families. Such gain in plasticity via longer durations of activity may also contribute to the population stability of the species over time. This trend interestingly occurred for all groups except for the parasitic bees (Fig. S3), which are the least likely group to be able to use a long phenological window to adjust their diet.

In regions with variable or unpredictable weather patterns, having a shorter phenological duration could disrupt bee foraging and nesting activities in years with atypical weather conditions, such as late frosts or extended dry periods. One study detected longer periods of low flowering abundance in the middle of the summer due to climate change (Aldridge et al. 2011), a predicament that could be buffered by a longer phenological window. The most common species with long durations were in Halictidae, the second-largest family of bees, which includes species with social behavioral attributes, including five of our social focal bee species (Fig. 5B). Sociality may contribute to extended phenological duration in social groups due to the need to produce multiple broods or generations during a single season. This extension may lead to increased abundance and colony growth. The phenological timing of social insects is influenced by the needs of the colony, as different tasks, such as foraging, brood rearing, and nest construction, require specific timing; longer durations could buffer bees from fluctuations in these rates, helping the colony maintain a stable size (Howard and Jeanne 2004). Finally, a strong association between abundant bees and long phenological durations could be a hopeful sign for ecosystem health, signifying consistent and extended pollination services that contribute to overall ecosystem stability.

Bee phenological traits varied more with diet breadth than sociality.

Diet Breadth. Bees with distinct dietary preferences had divergent phenological patterns, emphasizing a potential connection between food specialization and timing of flight activity. Specialist bees had later onset, peak, and end of activity than generalist or cleptoparasitic bees. Later phenological windows in our focal dryland ecosystems may be due to greater plant synchronization, possibly indicating the importance of late-season plant species to the specialist bee community. In line with this hypothesis, some of the latest onset bee species were Diadasia megamorpha and Perdita austini, and they are known to visit a limited variety of late-season flowering plant genera including Sphaeralcea, Helianthus, Gutierrezia, and Baileya. In contrast, some of the earliest active bee species, Anthophora porterae and Melecta pacifica, are known to visit a broad range of host plants for resources. With unique temporal adaptations, such as the shift to later seasonality we detected here, specialist bees may avoid competition with generalist bees and other pollinators that forage on a broader range of plant species.

In prior studies on bee phenology, species composition of bee communities in drought shifted towards generalist species (Robert L. Minckley, Roulston, and Williams

2013). Later seasonality in specialist bees may be due to activity cues from seasonal monsoons implying that this dryland system could see less specialist bees in drier years. In our study, the duration of activity did not vary with diet breadth, which is contrary to a prior study that determined shorter temporal resource overlap increased the degree of specialization in bees due to limitations in dietary options, while bees with extended flight periods could generalize on a higher variety (Glaum et al. 2021). One study reported that the seasonal availability and palatability of food plants correlated to shifts in butterfly and moth phenology with the degree of shift depending on dietary preference (Altermatt 2010). As late-season desert plant availability and palatability change in response to climatic variability so too could our desert bee community based on their dietary preferences (Zachmann et al. 2021).

Sociality. Social bees broadly had longer activity durations than solitary bees, implying another association between life history traits and phenology. Social bees are known to cache resources (Bryan N. Danforth et al. 2019), the acquisition of which over an extended period of inclement weather could buffer against reduced reproductive productivity, as seen in some solitary species. For instance, food limitation directly reduced the rate of brood rearing in the solitary bee Osmia pumila (Goodell 2003). This finding aligns with our hypothesis that social bees require longer durations than solitary bees to acquire sufficient resources to form colonies.

A longer phenological duration is likely advantageous for social bees because it aligns with their complex colony structure, division of labor, resource storage, and adaptability to environmental factors. It allows social bee colonies to function as highly organized and resilient societies, capable of thriving in dynamic and changing environments, a concept that has been well-studied in honeybees but remains understudied in native bees (Ulgezen, van Dooremalen, and van Langevelde 2021).Additionally, a longer phenological duration may enable social bees to collect and store larger quantities of resources, such as nectar and pollen, which can be crucial for sustaining the colony during periods of resource scarcity (Ejsmond et al. 2018). This strategy would buffer social bee colonies against environmental fluctuations impacting floral phenology. Their longer activity periods would also increase the duration of their pollination services, which can benefit the plants they visit by enhancing pollination success (Benedek et al. 2006).

Phenological traits strongly tracked bee evolutionary history.

By detecting the phylogenetic conservatism of phenological traits, we can use knowledge of well-studied taxa to predict the phenologies of unstudied taxa better. While our study is limited to only 74 bee taxa, we benefited from a long time series to determine phenological traits with high precision. Here, we revealed that phylogenetic signal in all phenological traits via all metrics of signal was robust, suggesting that phenological traits could be inferred for other species in the genera studied here. Studies have observed functional trait and phylogenetic diversity responses to specific environments, but less is known about phenological traits specifically (Hoiss et al. 2012; Villalta et al. 2022; Odanaka and Rehan 2019). Future work would benefit from expanding the scope of species and habitats examined to determine how generalizable such phylogenetic conservatism is across the full bee tree of life.

Phylogenetic patterns in bee phenological traits could emerge from the evolution of different phenological strategies to reduce competition for resources, such as nesting sites or nectar and pollen, due to variability in plant phenology (Stemkovski et al. 2023). Although it is typically assumed that competition is most intense among species within the same genus, interestingly, the phylogenetic patterns we detected suggest that competition as a driver of divergence would have occurred at higher taxonomic levels or during the divergence of genera rather than species within genera, because most genera had similar phenological traits. The species that were exceptions within their genus may be particularly interesting to investigate further, for example, Eucera lycii and Eucera territella in the genus Eucera in contrast to related genera Diadasia, Martinapis, Svastra, and Melissodes. Beyond these few exceptions, the phylogenetic patterns we detected did not support the hypothesis that closely related bee species that co-occur in the same habitat adapt their phenological timing to minimize competition for similar resources.

Of the 16 genera with more than one species represented, ten groups shared the same trend. These trends suggest that evolutionary history influences bee phenology, possibly due to dietary limitations. It is documented that host-plant associations appear to be determined by floral morphology and/or pollen chemistry, and that specialization was the primitive state for many bee groups (Bryan N. Danforth et al. 2013), which potentially limits the short-term plasticity of specialist clades due to their evolutionary history, causing them to be active in phenological unison. Many bee species have evolved in close association with specific host plants for foraging (Schlindwein, Pick, and Martins 2009). For example, focal bees in the genus Perdita, the majority of which are specialists, all trended toward later seasonality which implies they may have evolved to emerge later in the season to coincide with the availability of their host plants' flowers. By detecting phylogenetic conservatism in a particular group’s phenology, Perdita in this instance, we may be able to infer the phenology of other related taxa lacking data due to small sample sizes.

CONCLUSION

Our analysis of 16 years of monthly bee monitoring data for 74 bee species in the drylands of central New Mexico emphasizes the complex interplay of biological, environmental, and evolutionary factors in shaping bee phenological traits. The study provides valuable insights into the sensitivity of these traits to precipitation, which can be used to predict temporal shifts in community response with drier and warmer climates shifting phenological onset, peak, and end earlier in certain bee species. We have also emphasized the importance of long phenological durations for bee abundance and temporal stability, suggesting that bees with short durations are going to be most sensitive to declines in future climates, and both generalist and social bees may be able to resist or recover from climate change if they have long activity durations. Lastly, understanding bee evolutionary history may prove helpful in predicting vital bee phenological traits in understudied species to aid conservation efforts. Altogether, our work reveals new patterns in bee phenology that may aid the management of native dryland bee populations under threat of disruption by ongoing climate change.

APPENDIX 1: FIGURES

Figure 1.

Records of the month(s) of occurrence observed for each bee species during 2002-2019 across three ecosystem types of the Sevilleta National Wildlife Refuge, Socorro County, New Mexico. Species are organized and color-coded by family to depict the large diversity in phenological patterns within clades. Point sizes indicate the proportion of years in which each species was observed in each month.

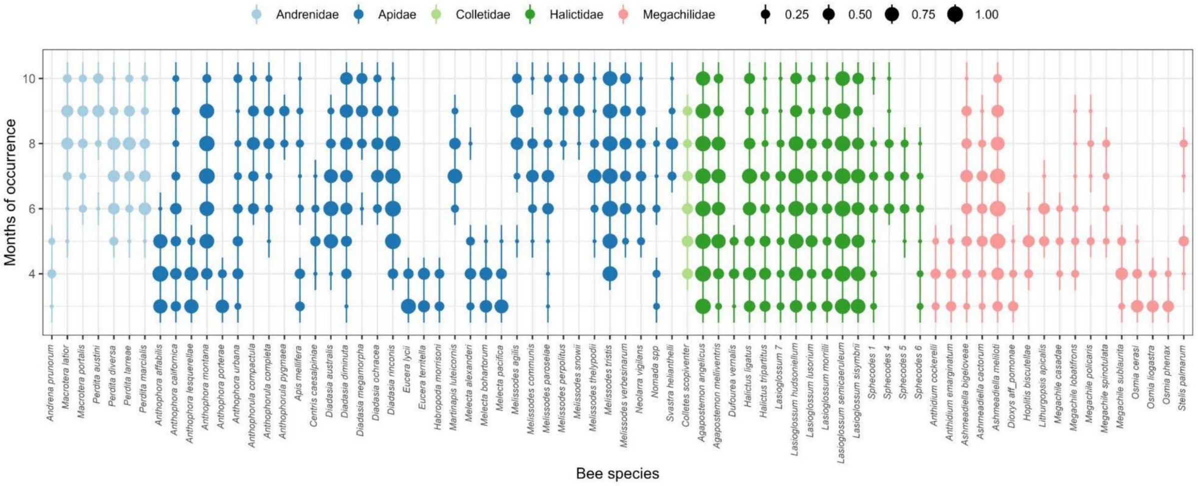


Figure 2.

Heat maps of phenological variability within a species for the 10 most common bee species during 2002 - 2019. Displayed as monthly bee species relative flight activity [*ln*(mean abundance + 1) in passive bee traps], averaged over three ecosystems of the Sevilleta National Wildlife Refuge, Socorro County, New Mexico.

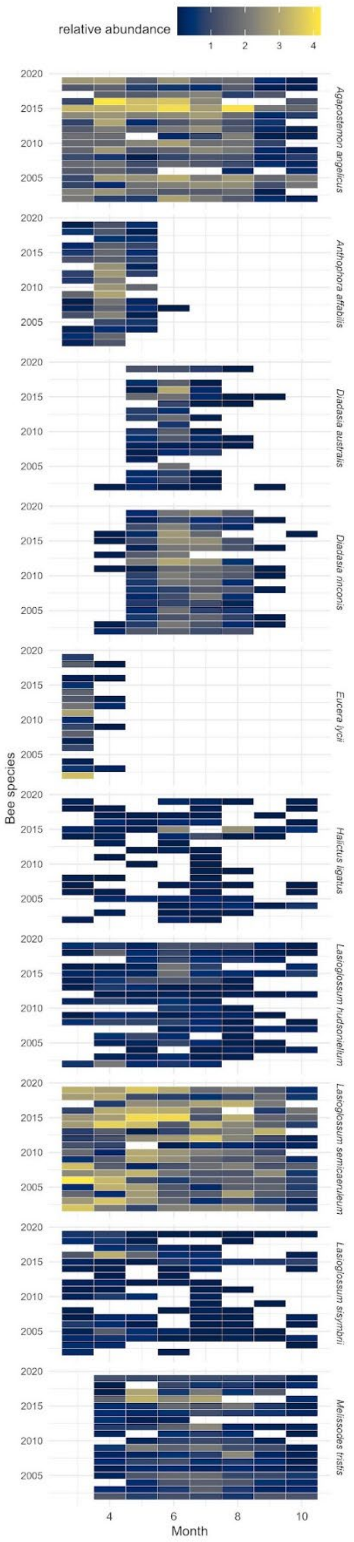


Figure 3.

Relative climate sensitivity of phenological traits to mean annual precipitation including (a) onset of activity, (b) peak activity, (c) end of activity, and (d) duration of activity of bee species. Points indicate the value of the slope (β) of the phenological trait against the yearly climate variable, standardized to mean = 0 and standard deviation = 1 (n = 16 years per species). Points were colored by the identity of the family of the bee species. The size of the points indicates the level of statistical significance of the climate sensitivity (P value for test of β = 0).

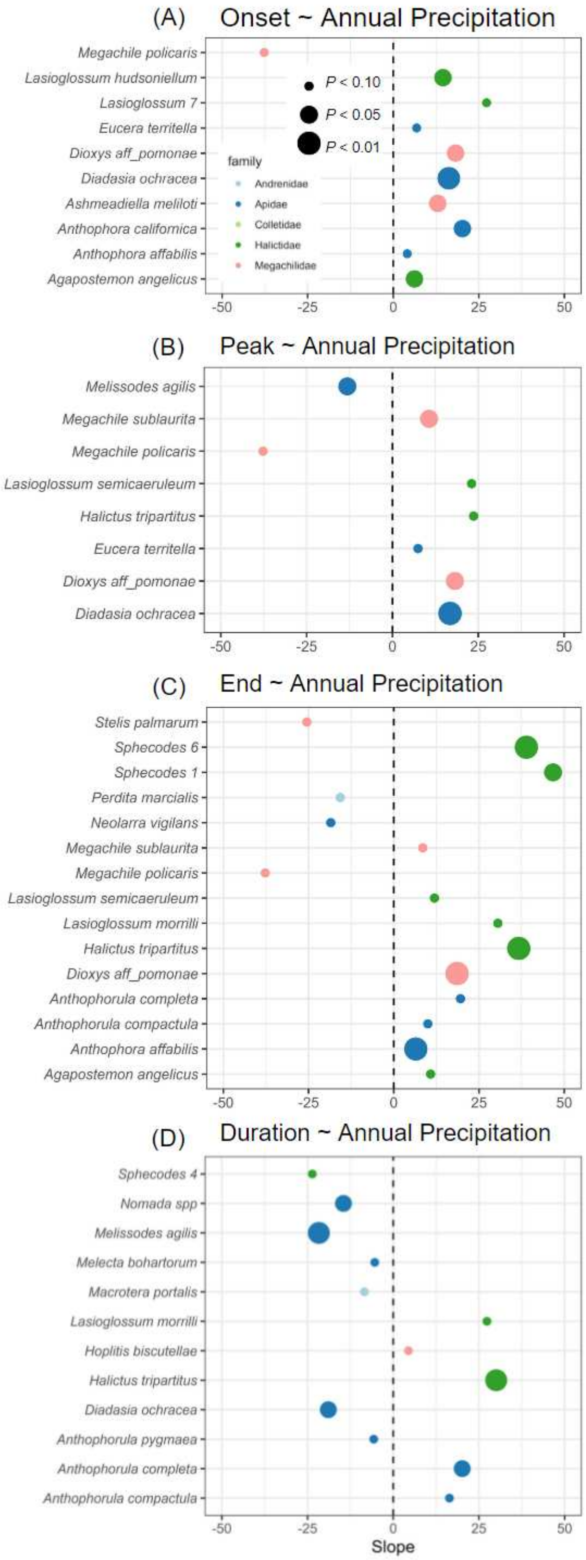
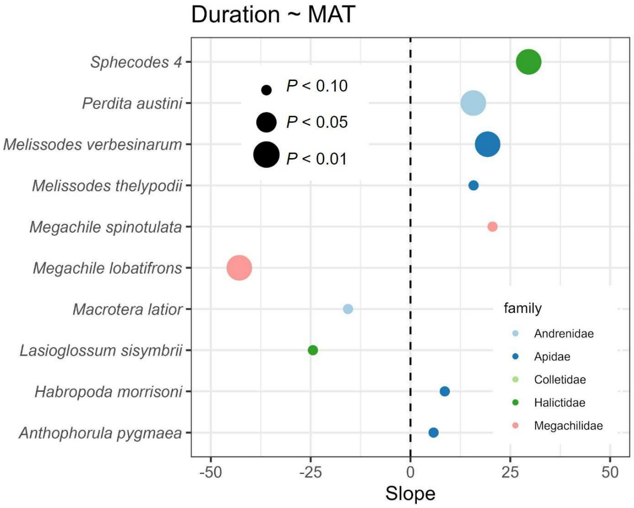


Figure 4.

Relative climate sensitivity of the phenological trait of duration to mean annual temperature. Points indicate the value of the slope (β) of duration against temperature, standardized to mean = 0 and standard deviation = 1 (n = 16 years per species). Points were colored by the identity of the family of the bee species. The size of the points indicates the level of statistical significance of the climate sensitivity (P value for test of $\beta = 0$).



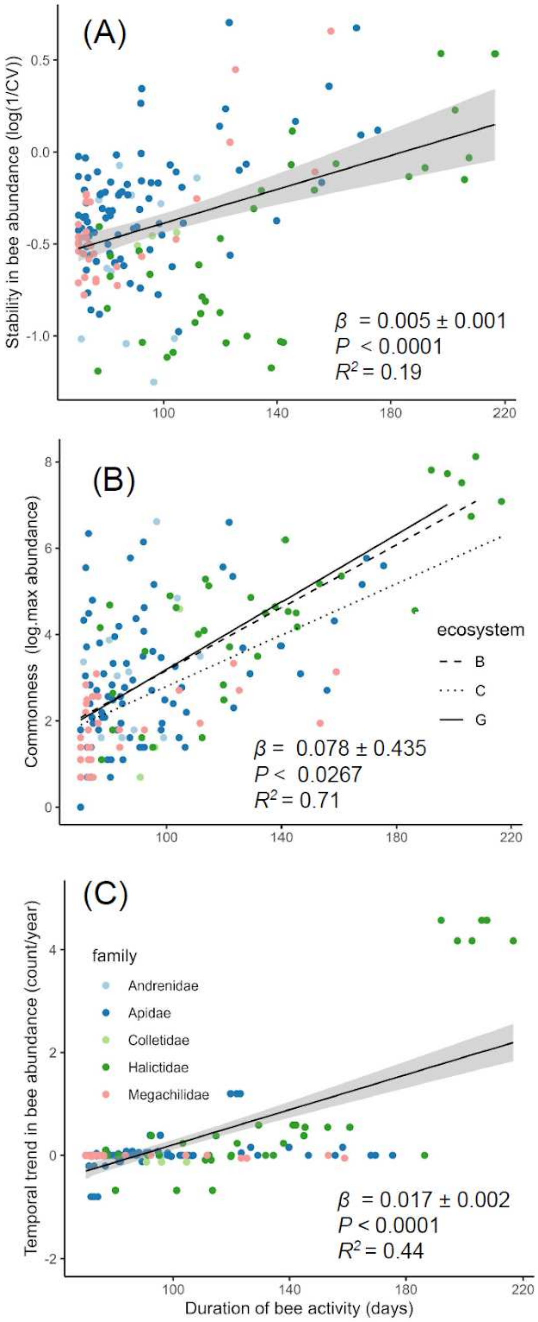


Figure 5.

Duration of bee activity was the best predictor of bee abundance metrics including (a) temporal stability in abundance as 1/CV of abundance over time, (b) commonness to rarity as log(max abundance over time), with significant ecosystem relationships being represented by varying line type and (c) the temporal trend in abundance as the slope (β) of change in abundance over time. Points were colored by the identity of the family of the bee species, lines show the slope of the linear regression, and shading indicates the 95% confidence interval around the slope.

Figure 6.

Variation in the timing of phenological traits among bee species with different diet breadth, showing mean (± s.e.) for (A) duration (in days), and (B) start, (C) peak, or (D) end of activity (in day of year). Different letters denote significant differences among diet breadth categories for each phenological trait.

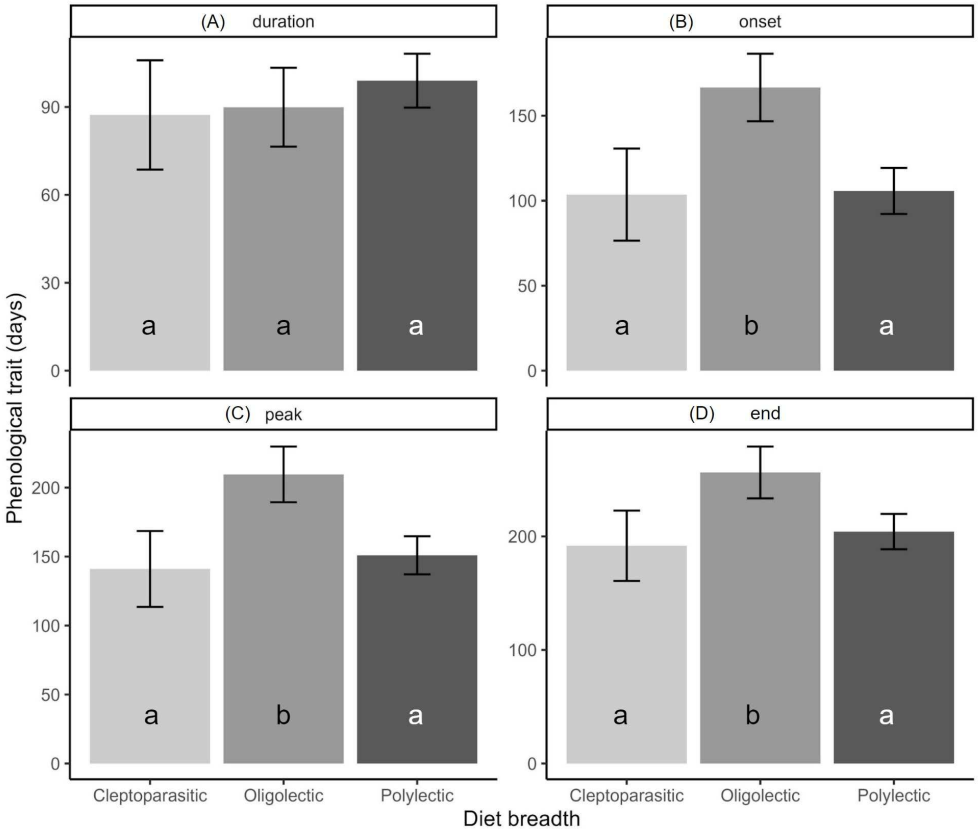
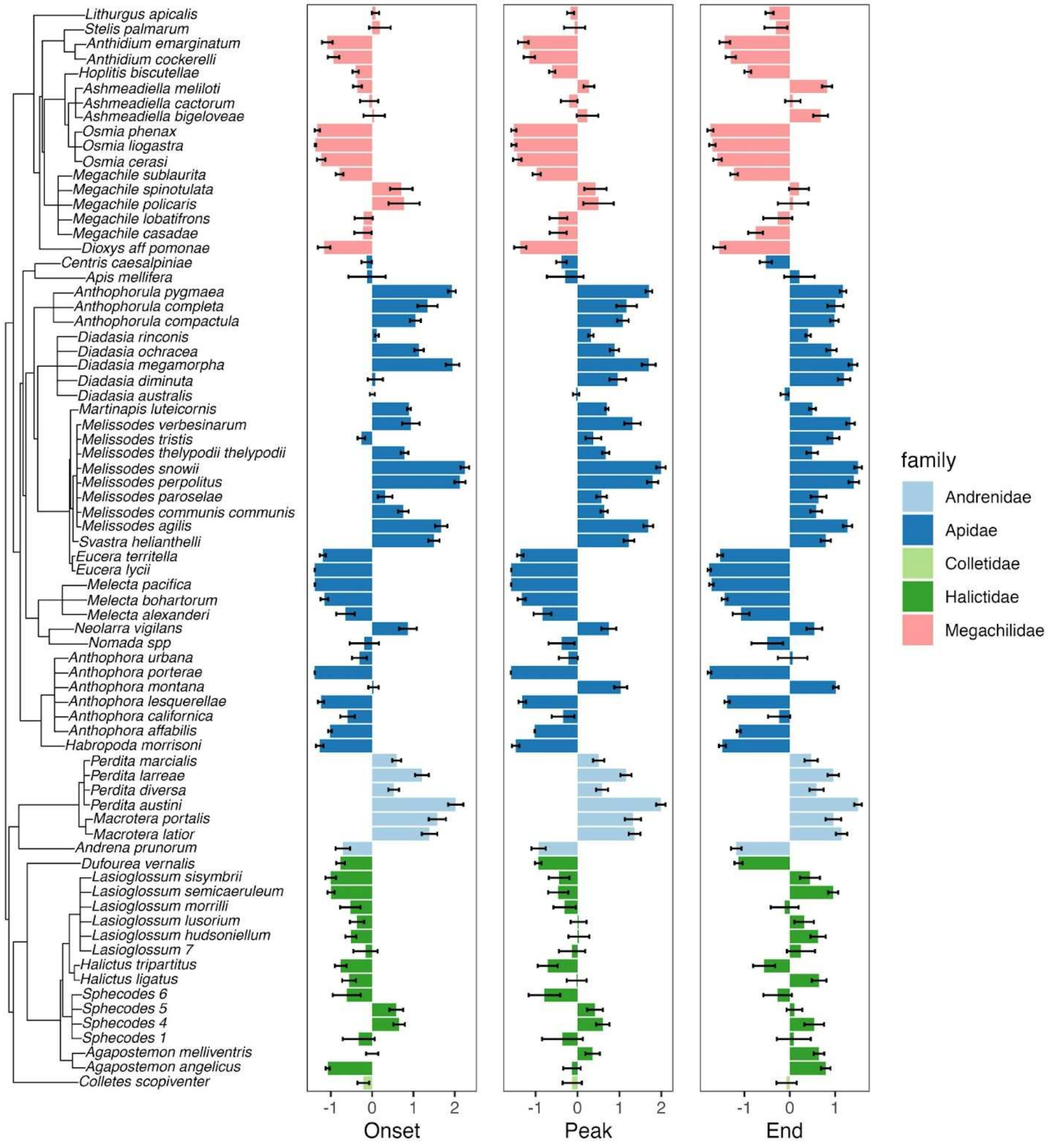


Figure 7.

Phylogeny of the focal bee species mapping the mean phenological traits of onset, peak, and end of activity (± s.e.), with 0 indicating the center date during the possible period of activity (in days) such that earlier phenology is to the left and later phenology is to the right. The color of bars identifies the family of the bee species.



APPENDIX 2: SUPPLEMENTARY MATERIALS

Table S1.

List of focal bee species for analysis.

Family	**Genus**	**Species**	**Diet breadth**	**Sociality**	**Mean onset**	**Mean peak**	**Mean end**	**Mean duration**
Andrenidae	*Andrena*	*prunorum*	Polylectic	Solitary	80.3	115.2	154.0	73.7
Andrenidae	*Macrotera*	*latior*	Oligolectic	Solitary	188.0	237.4	288.5	100.5
Andrenidae	*Macrotera*	*portalis*	Oligolectic	Solitary	197.8	235.2	278.1	80.3
Andrenidae	*Perdita*	*austini*	Oligolectic	Solitary	220.6	270.8	309.5	88.9
Andrenidae	*Perdita*	*diversa*	Oligolectic	Solitary	143.6	196.0	256.6	113.0
Andrenidae	*Perdita*	*larreae*	Oligolectic	Solitary	178.6	226.4	277.9	99.3
Andrenidae	*Perdita*	*marcialis*	Polylectic	Solitary	147.3	191.6	249.6	102.4
Apidae	*Anthophorula*	*compactula*	Polylectic	Solitary	170.5	222.5	279.3	108.8
Apidae	*Anthophorula*	*completa*	Polylectic	Solitary	185.6	227.2	280.7	95.1
Apidae	*Anthophorula*	*pygmaea*	Oligolectic	Solitary	215.9	255.6	290.3	74.4
Apidae	*Anthophora*	*affabilis*	Polylectic	Solitary	64.3	110.2	157.2	92.8
Apidae	*Anthophora*	*californica*	Polylectic	Solitary	86.1	146.3	208.7	122.5
Apidae	*Anthophora*	*lesquerellae*	Polylectic	Solitary	53.2	94.3	142.2	89.0
Apidae	*Anthophora*	*montana*	Polylectic	Solitary	118.4	219.7	281.2	162.8
Apidae	*Anthophora*	*porterae*	Polylectic	Solitary	45.3	80.0	119.6	74.3
Apidae	*Anthophora*	*urbana*	Polylectic	Solitary	101.0	153.1	226.0	125.0
Apidae	*Apis*	*mellifera*	Polylectic	Social	110.5	149.1	234.6	124.2
Apidae	*Centris*	*caesalpiniae*	Polylectic	Solitary	110.0	144.3	191.8	81.8

Apidae	*Diadasia*	*australis*	Oligolectic	Solitary	117.0	162.8	215.8	98.8
Apidae	*Diadasia*	*diminuta*	Oligolectic	Solitary	120.8	215.9	291.6	170.9
Apidae	*Diadasia*	*megamorpha*	Oligolectic	Solitary	216.7	255.4	303.1	86.4
Apidae	*Diadasia*	*ochracea*	Oligolectic	Solitary	175.0	211.8	275.6	100.6
Apidae	*Diadasia*	*rinconis*	Oligolectic	Solitary	122.6	181.7	245.8	123.2
Apidae	*Eucera*	*lycii*	Polylectic	Solitary	45.3	80.2	119.1	73.8
Apidae	*Eucera*	*territella*	Polylectic	Solitary	55.4	91.8	133.4	78.0
Apidae	*Habropoda*	*morrisoni*	Polylectic	Solitary	51.7	86.0	136.3	84.7
Apidae	*Martinapis*	*luteicornis*	Polylectic	Solitary	162.5	202.1	251.4	88.9
Apidae	*Melecta*	*alexanderi*	Cleptoparasitic	Parasitic	83.6	120.2	160.2	76.6
Apidae	*Melecta*	*bohartorum*	Cleptoparasitic	Parasitic	57.5	93.6	139.1	81.6
Apidae	*Melecta*	*pacifica*	Cleptoparasitic	Parasitic	45.5	80.2	122.2	76.7
Apidae	*Melissodes*	*agilis*	Oligolectic	Solitary	202.5	254.8	296.3	93.8
Apidae	*Melissodes*	*communis*	Polylectic	Solitary	155.5	198.6	256.1	100.6
Apidae	*Melissodes*	*paroselae*	Polylectic	Solitary	132.9	195.3	259.2	126.2
Apidae	*Melissodes*	*perpolitus*	Oligolectic	Solitary	225.9	260.3	304.1	78.2
Apidae	*Melissodes*	*snowii*	Polylectic	Solitary	232.0	270.9	309.6	77.6
Apidae	*Melissodes*	*thelypodii*	Polylectic	Solitary	157.0	200.6	250.9	93.9
Apidae	*Melissodes*	*tristis*	Polylectic	Solitary	103.4	184.9	278.1	174.7
Apidae	*Melissodes*	*verbesinarum*	Oligolectic	Solitary	164.9	234.7	299.9	135.1
Apidae	*Neolarra*	*vigilans*	Cleptoparasitic	Parasitic	161.2	204.6	253.8	92.5
Apidae	*Nomada*	*spp*	Cleptoparasiti	Parasitic	107.0	144.4	193.6	86.6

			c					
Apidae	*Svastra*	*helianthelli*	Oligolectic	Solitary	193.5	230.2	268.3	74.8
Colletidae	*Colletes*	*scopiventer*	Oligolectic	Solitary	105.8	157.9	218.2	112.4
Halictidae	*Agapostemon*	*angelicus*	Polylectic	Communal	61.6	157.7	268.3	206.7
Halictidae	*Agapostemon*	*melliventris*	Polylectic	Communal	116.8	183.9	259.6	142.9
Halictidae	*Dufourea*	*vernalis*	Polylectic	Solitary	77.4	114.7	156.9	79.4
Halictidae	*Halictus*	*ligatus*	Polylectic	Social	88.1	163.7	259.8	171.7
Halictidae	*Halictus*	*tripartitus*	Polylectic	Social	77.8	126.8	189.6	111.8
Halictidae	*Lasioglossum*	*7*	Polylectic	Social	108.5	157.8	236.6	128.1
Halictidae	*Lasioglossum*	*hudsoniellum*	Polylectic	Social	90.3	166.5	258.6	168.2
Halictidae	*Lasioglossum*	*lusorium*	Oligolectic	Solitary	98.0	166.1	240.7	142.7
Halictidae	*Lasioglossum*	*morrilli*	Polylectic	Solitary	89.6	148.2	215.8	126.2
Halictidae	*Lasioglossum*	*semicaeruleum*	Polylectic	Social	65.7	140.2	277.7	212.0
Halictidae	*Lasioglossum*	*sisymbrii*	Polylectic	Solitary	65.3	141.3	248.2	182.8
Halictidae	*Sphecodes*	*1*	Cleptoparasitic	Parasitic	100.0	145.5	227.5	127.5
Halictidae	*Sphecodes*	*4*	Cleptoparasitic	Parasitic	150.3	196.9	253.5	103.3
Halictidae	*Sphecodes*	*5*	Cleptoparasitic	Parasitic	146.8	187.0	228.3	81.6
Halictidae	*Sphecodes*	*6*	Cleptoparasitic	Parasitic	85.2	122.6	206.8	121.6
Megachilidae	*Anthidium*	*cockerelli*	Polylectic	Solitary	68.8	103.4	147.0	78.3
Megachilidae	*Anthidium*	*emarginatum*	Polylectic	Solitary	61.0	95.6	139.3	78.3
Megachilidae	*Ashmeadiella*	*bigeloveae*	Polylectic	Solitary	119.2	177.3	261.8	142.5

Megachilidae	*Ashmeadiella*	*cactorum*	Polylectic	Solitary	113.1	154.2	226.2	113.1
Megachilidae	*Ashmeadiella*	*meliloti*	Polylectic	Solitary	98.5	179.3	270.0	171.5
Megachilidae	*Dioxys*	*aff_pomonae*	Cleptoparasitic	Parasitic	57.0	91.8	132.3	75.3
Megachilidae	*Hoplitis*	*biscutellae*	Oligolectic	Solitary	96.3	132.5	168.8	72.5
Megachilidae	*Lithurgopsis*	*apicalis*	Oligolectic	Solitary	121.0	155.8	196.5	75.5
Megachilidae	*Megachile*	*casadae*	Oligolectic	Solitary	105.3	140.2	178.7	73.3
Megachilidae	*Megachile*	*lobatifrons*	Polylectic	Solitary	106.3	140.4	207.0	100.8
Megachilidae	*Megachile*	*policaris*	Polylectic	Solitary	156.4	191.4	226.4	70.0
Megachilidae	*Megachile*	*spinotulata*	Polylectic	Solitary	153.0	187.6	234.1	81.1
Megachilidae	*Megachile*	*sublaurita*	Polylectic	Solitary	76.2	112.7	151.2	74.9
Megachilidae	*Osmia*	*cerasi*	Polylectic	Solitary	53.3	88.0	129.9	76.6
Megachilidae	*Osmia*	*liogastra*	Polylectic	Solitary	46.2	83.7	123.3	77.1
Megachilidae	*Osmia*	*phenax*	Polylectic	Solitary	48.6	83.4	120.8	72.2
Megachilidae	*Stelis*	*palmarum*	Cleptoparasitic	Parasitic	126.4	161.0	204.6	78.2

Table S2.

Parameter estimates for climate sensitivity of bee species phenological traits, providing all species with climate relationships of $P > 0.1$. Species with significant trends at $P < 0.05$ are highlighted in bold.

Bee species	**Slope**	***P*-value**	***P* category**	**Phenological trait**	**Climate variable**
Macrotera portalis	-8.4	0.0827	<0.1	duration	precipitation
Perdita marcialis	-15.7	0.0719	<0.1	end	precipitation
Anthophorula compactula	16.4	0.0787	<0.1	duration	precipitation
Anthophorula compactula	10.0	0.0749	<0.1	end	precipitation
Anthophorula completa	19.6	0.0615	<0.1	end	precipitation
Anthophorula completa	20.1	**0.0146**	<0.05	duration	precipitation
Anthophorula pygmaea	-5.7	0.0645	<0.1	duration	precipitation
Anthophora affabilis	4.1	0.0680	<0.1	start	precipitation
Anthophora affabilis	6.5	**0.0065**	<0.01	end	precipitation
Anthophora affabilis	0.4	0.0913	<0.1	peak	precipitation
Anthophora californica	20.2	**0.0240**	<0.05	start	precipitation
Diadasia ochracea	16.2	**0.0028**	<0.01	start	precipitation
Diadasia ochracea	16.8	**0.0017**	<0.01	peak	precipitation
Diadasia ochracea	-18.9	**0.0124**	<0.05	duration	precipitation
Eucera territella	7.4	0.0762	<0.1	peak	precipitation

Bee species	**Slope**	***P*-value**	***P* category**	**Phenological trait**	**Climate variable**
Eucera territella	6.8	0.0822	<0.1	start	precipitation
Melecta bohartorum	-5.4	0.0617	<0.1	duration	precipitation
Melecta pacifica	0.4	0.0886	<0.1	peak	precipitation
Melissodes agilis	-21.7	**0.0076**	<0.01	duration	precipitation
Melissodes agilis	-13.2	**0.0328**	<0.05	peak	precipitation
Neolarra vigilans	-18.5	0.0759	<0.1	end	precipitation
Nomada spp	-14.5	**0.0441**	<0.05	duration	precipitation
Agapostemon angelicus	10.8	0.0789	<0.1	end	precipitation
Agapostemon angelicus	6.2	**0.0120**	<0.05	start	precipitation
Halictus tripartitus	30.0	**0.0071**	<0.01	duration	precipitation
Halictus tripartitus	23.7	0.0709	<0.1	peak	precipitation
Halictus tripartitus	36.7	**0.0060**	<0.01	end	precipitation
Lasioglossum 7	27.3	0.0854	<0.1	start	precipitation
Lasioglossum hudsoniellum	14.5	**0.0334**	<0.05	start	precipitation
Lasioglossum morrilli	27.3	0.0975	<0.1	duration	precipitation
Lasioglossum morrilli	30.6	0.0983	<0.1	end	precipitation
Lasioglossum semicaeruleum	23.1	0.0823	<0.1	peak	precipitation
Lasioglossum semicaeruleum	11.9	0.0671	<0.1	end	precipitation
Sphecodes 1	46.7	**0.0215**	<0.05	end	precipitation
Sphecodes 4	-23.6	0.0956	<0.1	duration	precipitation
Sphecodes 6	38.9	**0.0097**	<0.01	end	precipitation

Bee species	**Slope**	***P*-value**	***P* category**	**Phenological trait**	**Climate variable**
Ashmeadiella meliloti	13.0	**0.0158**	<0.05	start	precipitation
Dioxys aff_pomonae	18.2	**0.0117**	<0.05	peak	precipitation
Dioxys aff_pomonae	18.6	**0.0063**	<0.01	end	precipitation
Dioxys aff_pomonae	18.2	**0.0107**	<0.05	start	precipitation
Hoplitis biscutellae	4.4	0.0891	<0.1	duration	precipitation
Megachile policaris	-37.7	0.0587	<0.1	peak	precipitation
Megachile policaris	-37.7	0.0587	<0.1	end	precipitation
Megachile policaris	-37.7	0.0587	<0.1	start	precipitation
Megachile sublaurita	8.5	0.0924	<0.1	end	precipitation
Megachile sublaurita	10.7	**0.0415**	<0.05	peak	precipitation
Stelis palmarum	-25.5	0.0992	<0.1	end	precipitation
Macrotera latior	-15.6	0.0749	<0.1	duration	temperature
Perdita austini	15.7	**0.0190**	<0.05	duration	temperature
Perdita austini	-21.6	**0.0185**	<0.05	start	temperature
Anthophorula pygmaea	5.8	0.0583	<0.1	duration	temperature
Diadasia megamorpha	10.1	0.0795	<0.1	end	temperature
Habropoda morrisoni	-9.2	0.0555	<0.1	start	temperature
Habropoda morrisoni	-9.6	**0.0488**	<0.05	peak	temperature
Habropoda morrisoni	8.6	0.0825	<0.1	duration	temperature
Melissodes thelypodii	14.8	**0.0465**	<0.05	end	temperature
Melissodes thelypodii	15.8	0.0815	<0.1	duration	temperature

Bee species	**Slope**	***P*-value**	***P* category**	**Phenological trait**	**Climate variable**
Melissodes verbesinarum	19.3	**0.0499**	<0.05	duration	temperature
Dufourea vernalis	8.5	**0.0471**	<0.05	peak	temperature
Lasioglossum 7	-38.0	**0.0061**	<0.01	start	temperature
Lasioglossum 7	-35.2	0.0559	<0.1	end	temperature
Lasioglossum sisymbrii	-23.8	0.0687	<0.1	end	temperature
Lasioglossum sisymbrii	-24.4	0.0778	<0.1	duration	temperature
Sphecodes 4	29.6	**0.0205**	<0.05	duration	temperature
Ashmeadiella meliloti	-12.0	0.0877	<0.1	peak	temperature
Megachile lobatifrons	-35.0	0.0696	<0.1	end	temperature
Megachile lobatifrons	-42.9	**0.0157**	<0.05	duration	temperature
Megachile spinotulata	20.6	0.0817	<0.1	duration	temperature
Osmia cerasi	-10.1	0.0636	<0.1	start	temperature
Osmia cerasi	-10.2	0.0636	<0.1	peak	temperature

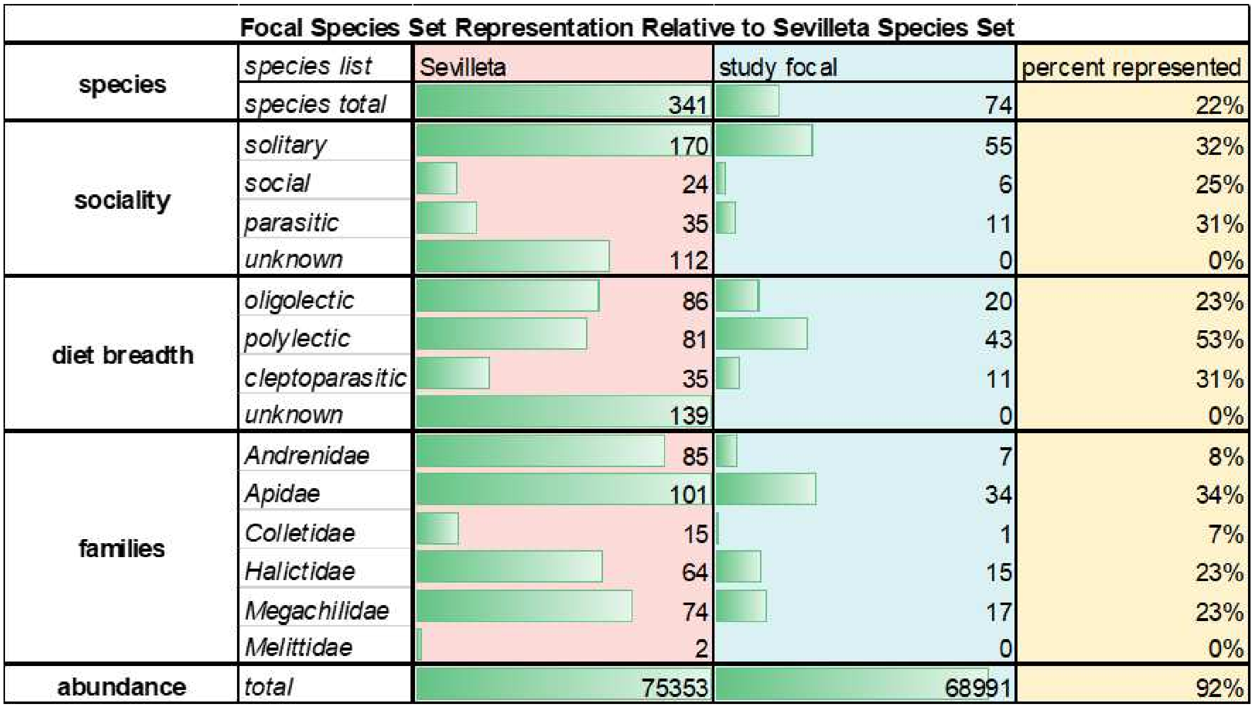
Table S3.

Results of model selection procedures comparing phenological traits as predictors of (a) temporal stability in bee abundance as 1/CV of abundance over time, (b) commonness-to-rarity as ln (mean abundance over time), or (c) winner vs. loser species over time as the slope of change in bee abundance over time.

Model Predictor	*AICc*	delta *AICc*
(a) *Temporal stability*		
Onset	79.7	22.3
Peak	79.4	22
End	75.9	18.5
Duration	57.4	0
(b) *Commonness-Rarity*		
Onset	505.4	61.2
Peak	521.8	77.6
End	523.5	79.3
Duration	444.2	0
(c) *Winner - Loser*		
Onset	420.3	93.4
Peak	423.3	96.4
End	411.7	84.8
Duration	326.9	0

Table S4.

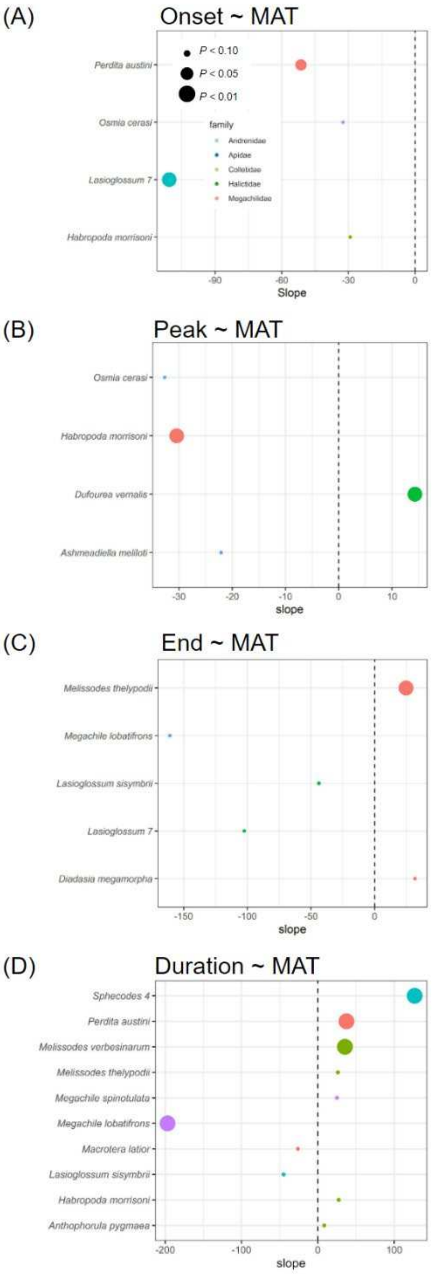
Summary of the representation of the focal set of bee species (74 species) for the full bee community (341 species).



	Focal Species Set Representation Relative to Sevilleta Species Set			
species	*species list*	Sevilleta	study focal	percent represented
	species total	341	74	22%
sociality	*solitary*	170	55	32%
	social	24	6	25%
	parasitic	35	11	31%
	unknown	112	0	0%
diet breadth	*oligolectic*	86	20	23%
	polylectic	81	43	53%
	cleptoparasitic	35	11	31%
	unknown	139	0	0%
families	*Andrenidae*	85	7	8%
	Apidae	101	34	34%
	Colletidae	15	1	7%
	Halictidae	64	15	23%
	Megachilidae	74	17	23%
	Melittidae	2	0	0%
abundance	*total*	75353	68991	92%

Figure S1.

Relative climate sensitivity of phenological traits to mean annual temperature including (a) onset of activity, (b) peak activity, (c) end of activity, and (d) duration of activity of bee species. Points indicate the value of the slope (β) of the phenological trait against the yearly climate variable, standardized to mean = 0 and standard deviation = 1 ($n = 18$ years per species). Points were colored by the identity of the family of the bee species. The size of the points indicates the level of statistical significance of the climate sensitivity (P value for test of $\beta = 0$).



We also evaluated whether diet breadth or sociality traits altered how phenological traits predicted bee population stability, commonness, or temporal trends in abundance (winners vs. losers over time). We used general linear mixed effects models that predicted *log*(stability) ~ phenological trait × life history trait. Bee species identity was included as a random effect to account for replicate observations of the same species in each of the three ecosystem types, and the mixed models were fit with maximum likelihood estimation using the lmer in package lme4 (Bates et al. 2015). Log transformation of stability improved the homogeneity of variances in the models. If interactions with the life history trait were significant , we tested for differences among life histories in the stability~phenology relationship using function pairs (emtrends) from the emmeans package (Lenth 2018).

Figure S2.

Temporal abundance trends calculated as the slope (β) of change in abundance over time were strongest for generalist (polylectic) bees. Points were colored by the identity of the family of the bee species, lines show the slope of the linear regression, and shading indicates the 95% confidence interval around the slope.

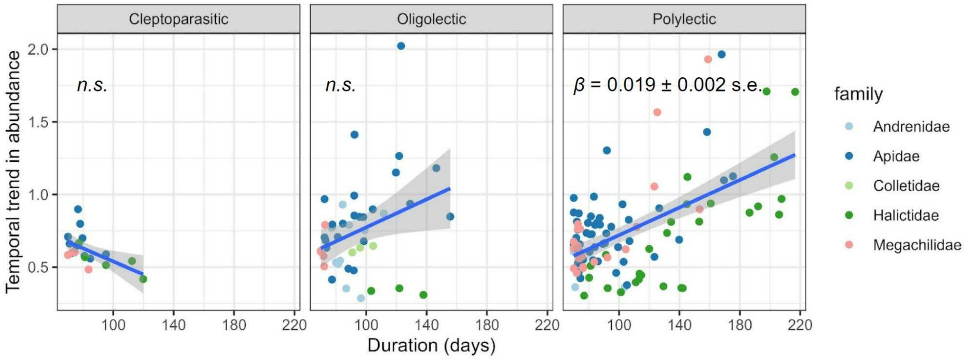
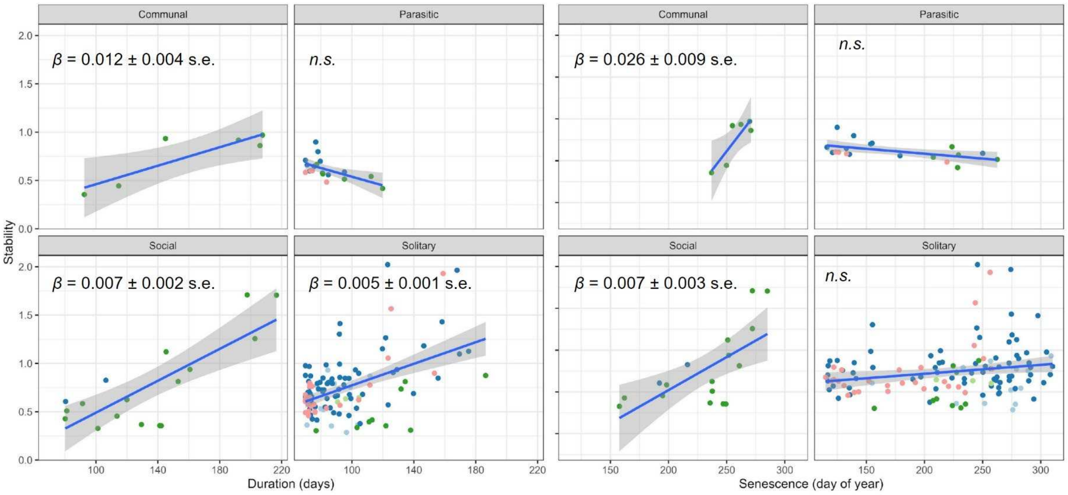


Figure S3.

Duration of bee activity predicts temporal stability, calculated as 1/CV of abundance over time, for all sociality groups with the exception of parasitic bees. A later end date of activity also predicted greater temporal stability in the abundance of communal and social bees. Points were colored by the identity of the family of the bee species, lines show the slope of the linear regression, and shading indicates the 95% confidence interval around the slope.



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