

# Temporal Patterns in Species Flowering in Sky Islands of the Sonoran Desert Ecoregion

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**Abstract**—Highly variable moisture conditions in the Sonoran Desert play a significant role in shaping the composition and phenology of plants in this water-limited region. The flowering patterns of plants of the Finger Rock trail, located in the Santa Catalina Mountains of southern Arizona, have been very carefully documented on approximately a weekly basis for nearly three decades. These observations, made along a gradient encompassing more than 4,000 ft in elevation, have revealed that flower presence, timing, and duration vary dramatically from year to year for many species in this unique environment.

We developed a daily probability of flowering estimate for each species from the empirical records of presence or absence of flowering and implemented a clustering algorithm to elucidate recurrent temporal flowering patterns among groups of species. Several patterns emerged, and these patterns are consistent with plant functional types. First, across the elevation gradient, over half of all species that have been documented exhibit very low (<10%) probabilities of flowering in any given year, a pattern that exemplifies the high degree of variability and opportunism in this water-limited environment. In addition, there are small groups of species that are consistently seen in flower nearly every year and at nearly the same day of year, regardless of the preceding or concurrent climate conditions. The reliability with which these species in these groups flower, both from year to year and at the same time every year, increases with increasing elevation, and is also higher in summer than in the spring season. Clusters comprised mainly of annual species tended to show lower flowering probabilities and therefore greater variability in flowering; the opposite was generally true for perennial and woody species. The baseline patterns established in this analysis enhance our current understanding of seasonal flowering patterns in this region and serve as a critical step toward understanding how the system may change under future climate conditions.

## Introduction

The Sonoran Desert is characterized by two distinct periods of flowering, one in spring and one in summer. However, the assemblage of species seen in flower in a particular season varies widely from year to year (Crimmins and others 2008). Similarly, though the coarse patterns of distinct spring and flowering seasons are consistent from year to year, the timing of species' flowering onset and the length of time individual species remain in flower can vary considerably.

In dry environments, precipitation is the dominant limiting factor, shaping species composition and productivity (Noy-Meir 1973; McClaran and Van Devender 1995) and playing a critical role in cue-

ing phenological events (Beatley 1974; Bowers and Dimmitt 1994; Crimmins and others 2010; Peñuelas and others 2004). However, the relationship between precipitation and plant phenology has generally been established either at a coarse level—for entire plant communities at the seasonal scale (e.g., Crimmins and others 2008)—or for small groups of species (e.g., Aronson and others 1992; Bowers and Dimmitt 1994; Kemp 1983; Kimball and others 2009). Therefore, we can make predictions regarding the flowering response in a given season at a coarse level, such as whether a spring season is likely to be a “good” wildflower year, characterized by abundant and diverse wildflower populations (e.g., Bowers 2005). On the other hand, we mostly lack the ability to make finer-scale predictions such as whether particular species are likely to be seen in flower, when they may initiate flowering, and what the duration of their flowering over the course of the season might be.

Datasets that capture the response of an entire biological community are rare, and repeated measurements of an entire system are even scarcer. Datasets that offer repeated measurements of an entire community are rich and valuable resources that can enhance our empirical understanding of species' responses within the larger ecosystem. In this study, we utilized a long-term record of flowering

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plant phenology of all species observed (encompassing over 600 taxa on a nearly weekly interval), which enabled us to explore in detail both the year-to-year patterns in flowering for individual species and each species' inter-annual variability in flowering onset and duration.

We use a dataset spanning 27 years to investigate variability and timing of flowering patterns within and spanning the distinct spring and summer seasons characteristic of the Sonoran Desert. Specifically, we asked from year to year, (1) how consistently do individual species flower; (2) how much does flowering onset and duration vary among species; and (3) are there patterns in flowering onset, duration, and inter-annual variability that are relatively consistent across species?

In this study, we evaluated temporal flowering across a 1200-m elevation gradient and explored the consistency of patterns across a moisture gradient encompassing xeric desert scrub to mesic pine forest communities. The findings of this evaluation can guide temporal sampling regimes for long-term monitoring to optimize the likelihood of observing particular species in flower and can also be used to identify peaks in flowering diversity. In addition, these results provide information on resource availability and habitat condition, which is valuable for wildlife species. Finally, this information can also serve as an important baseline from which to begin evaluations of how the system may change under future climate conditions.

## Methods

The data examined in this study include 136,036 observations of plants in flower for 601 species made by David Bertelsen. These data are the results of 1,243 round-trip (16 km) hikes of the route to Mt. Kimball, and 25 partial trips of 4.8–12.1 km made over a 27-year period (1984–2010), excluding 2004 and 2005, when the observer was unable to complete regular hikes ( $4.4 \pm 0.01$  hikes month<sup>-1</sup> [mean  $\pm$  SE]). The 8-km hiking route to Mt. Kimball is located on the south slope of the Santa Catalina Mountains, approximately 7 km north of the city limits of Tucson, Arizona, USA, and follows the Finger Rock and Pima Canyon trails. The observer recorded species observed in bloom within approximately 9.1 m of either side of the trail. Observations were recorded along five trail segments approximately 1 mile (1.6 km) in length both on the ascent and descent; on the descent attention was given to verifying records and adding any taxa not already recorded. Trail mile 1 refers to the lowest elevation segment; trail mile 5 refers to the highest elevation; further details regarding the study site and data collection methods are provided in Crimmins and others (2011). Each species was assigned to one of the following functional types: annual/biennial forbs, herbaceous perennials, and woody plants. Functional type groupings were selected based on the different water use strategies employed by plants of semi-arid environments (Burgess 1995; Ehleringer and others 1991).

To evaluate consistency of flowering on each calendar day from year to year, we calculated a "probability of species flowering" (PSF) for each day in the entire record (>9,800 days) for each species. This was done by first interpolating individual species flowering presence/absence observations collected at an irregular interval to a consistent daily matrix of 9,800 days. Changes in the flowering status (presence = 1 or absence = 0) were linearly interpolated between consecutive hikes with a mid-point value of 0.5. All days in the record with a value higher than 0.5 were converted to flowering days (presence = 1) for each species. The full data matrix of daily flowering occurrence was then used to calculate the empirical probability of occurrence for each day of the year. If a species was observed in multiple trail miles, observations specific to each mile were treated independently. The resultant species-mile PSFs provide us with the likelihood of a spe-

cies being observed in flower on each day of the year in a particular trail mile.

Several potential probability of flowering curves could arise from long time-series of phenological status observations. Examples of these and the structure of the input data responsible for these patterns appear in fig. 1. These models represent the extreme cases; we expect most curves would fall somewhere between one or more of these extremes. Individual species PSF plots provide information on several elements: the length of time, or **duration**, that a species is typically seen in flower, the year-to-year **consistency** in the days of year a species is seen in flower, and the **probability** of a species being observed in flower in a given year. The height and width of the peaks result from a combination of these features. Species associated with tall, narrow peaks (fig. 1a) are characterized by a short flowering duration, a high year-to-year consistency, and are seen in flower nearly every year. Species that exhibit a short flowering duration and high consistency but are seen infrequently have narrow, short peaks (fig. 1b). Species that flower in most years for a long duration with high consistency are represented by tall, wide peaks (fig. 1c). These lengthy, short peaks can arise by multiple pathways. First, species that exhibit a long flowering duration with high consistency but flower in few years produce this pattern (fig. 1d). Similarly, short peaks that stretch over a longer period can result from species that flower for short durations and exhibit low consistency, that is, their flowering periods from year to year are highly variable (fig. 1e).

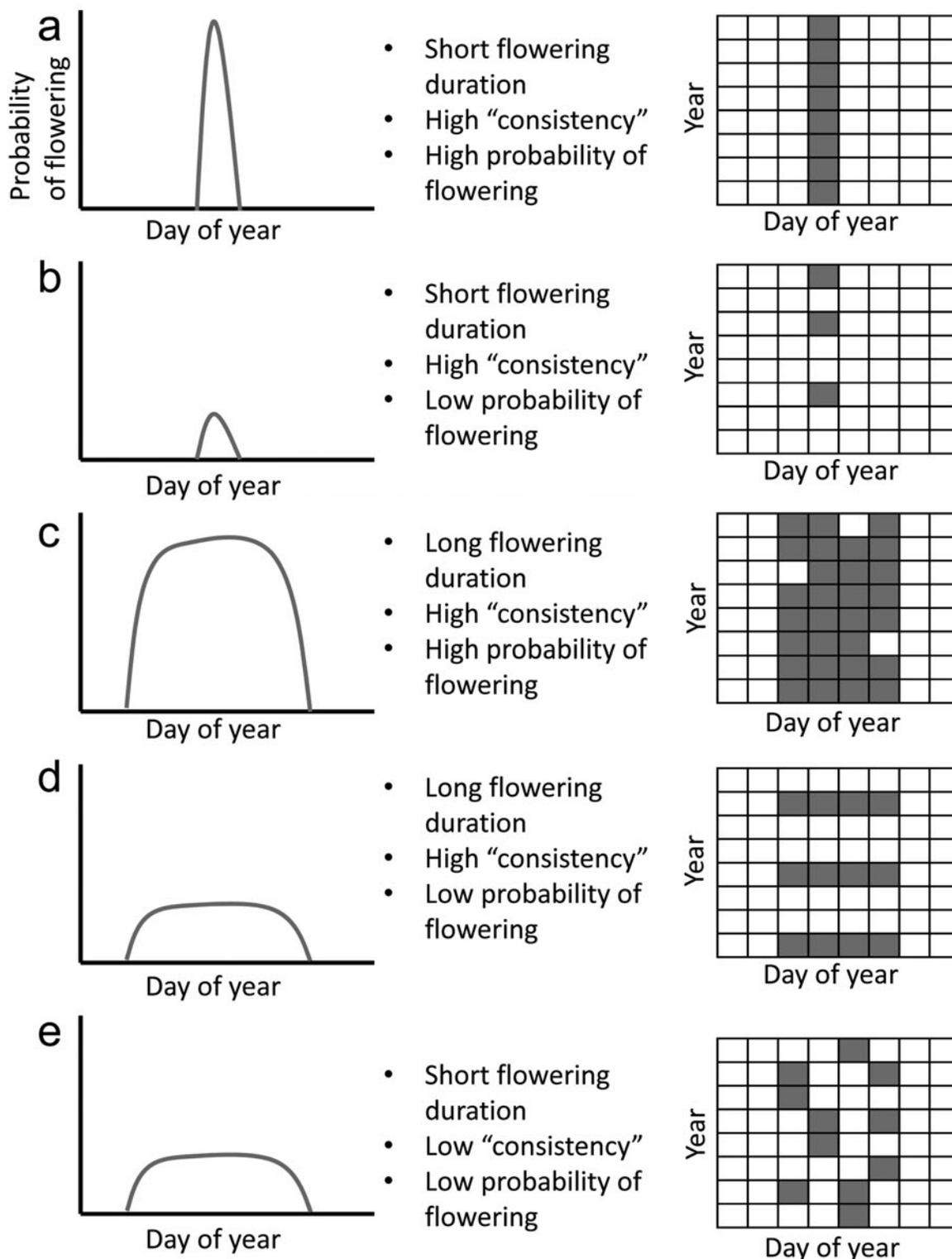
To collapse the individual 1,588 individual species-mile PSF curves into common flowering patterns, individual species' curves were clustered within each mile using a K-means algorithm using Matlab (R2011b). The algorithm uses five iterations of the K-means classifier and retains the clustering with the smallest sum squared error. To assess the optimal number of clusters for the input dataset, an ensemble of clusters ranging from 2 to 20 are generated and then compared using the Davies-Bouldin Index (DBI). A lower DBI indicates greater within-cluster similarity and greater separation between clusters. The smallest number of clusters with the lowest DBI value indicates the simplest efficient grouping of the input data. Seven clusters were retained for each trail mile based on these criteria.

## Results

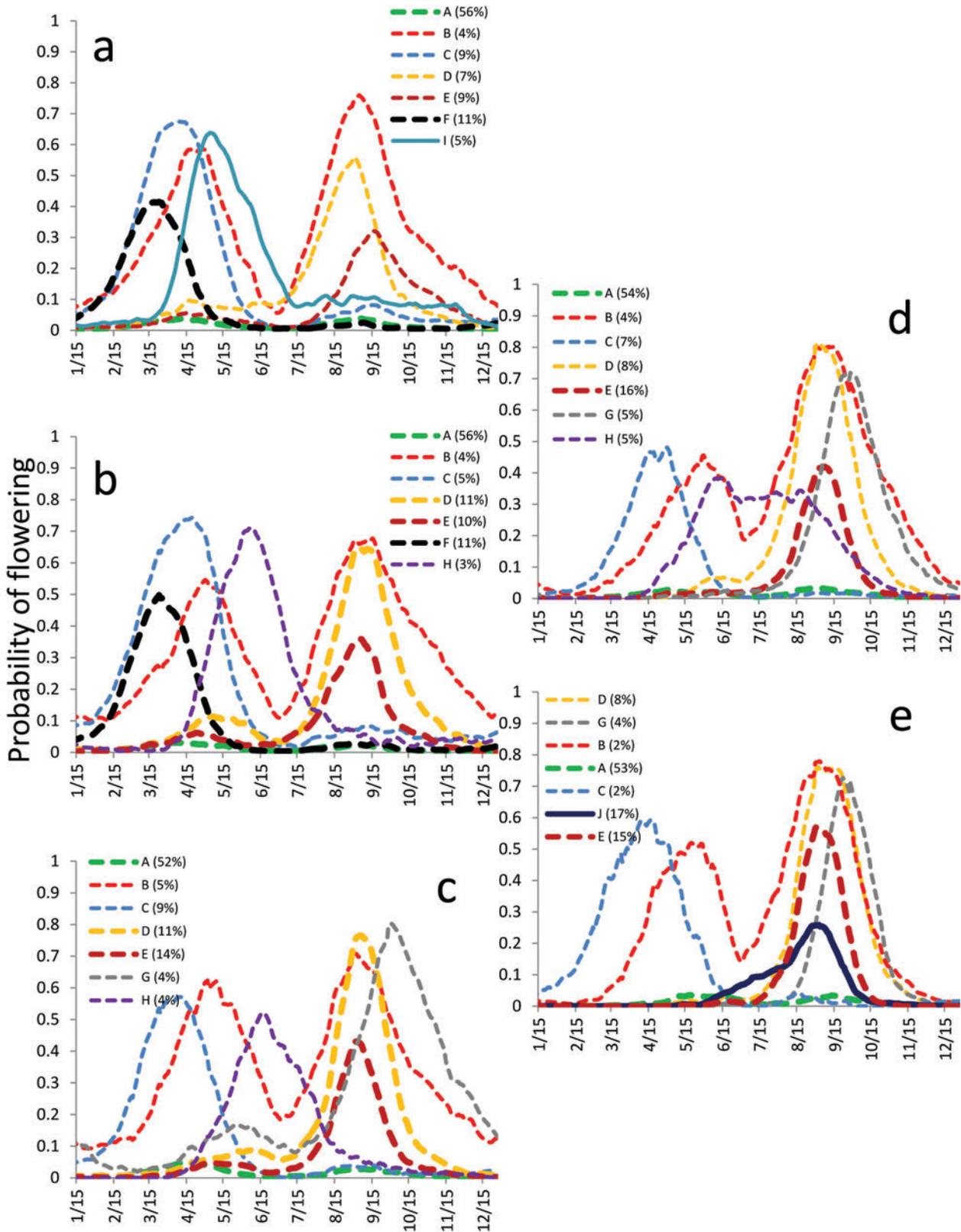
For each of the five trail miles we generated seven clusters (fig. 2), which represent patterns repeated across individual species' PSF plots. We identified 10 cluster patterns (labeled A–J), eight of which were consistent across multiple trail miles (fig. 2). Only cluster I (mile 1) and cluster J (mile 5) were unique to a single mile.

A very clear pattern is represented in cluster A, which is present in each of the five miles. Species associated with this cluster exhibit a very low probability of being seen in flower, and may flower over a very broad range of dates. This cluster encompasses greater than half of the species observed in each of the miles (table 1). The low probabilities associated with species in this cluster result from the comparatively small number of years observed in flower (average 5.7 to 6.9 years) (table 1). Accordingly, cluster A is comprised of many species that flower infrequently and unpredictably. These species may best be represented by model 1b (fig. 1).

Several other patterns were consistent across multiple trail miles. All miles were characterized by at least one spring-flowering cluster (clusters C or F), at least one summer-flowering cluster (clusters D, E, G, or J), and a bimodal flowering cluster (cluster B; fig. 2). Miles 1 and 2 exhibited multiple distinct spring peaks. Miles 2, 3, and 4 also exhibited a mid-year flowering cluster (cluster H), comprised primarily of succulents (table 1). Cluster peaks were generally higher



**Figure 1**—Conceptual model of potential probability of species flowering (PSF) models and the input data structure associated with these models. Potential PSF models appear in the left column; input data matrices appear in the right column. In the input data matrices, cells represent individual days of the year across a series of years. Observations of a species in flower are represented by cells shaded gray; observations of no flower are represented by unshaded cells. (a) a species that flowers in most years, for a short duration and with high consistency in year-to-year timing; (b) a species that flowers infrequently, with a short flowering duration, and with high year-to-year consistency in timing; (c) a species that flowers in most years, with high year-to-year consistency in timing, and for a long duration; (d) a species that flowers infrequently, with high year-to-year consistency in timing, and for a long duration; (e) a species that flowers for a short duration and with low year-to-year consistency in timing.



**Figure 2**—Probability of species occurrence plots for 5 trail miles. (a) mile 1; (b) mile 2; (c) mile 3; (d) mile 4; (e) mile 5. Dashed lines indicate that the cluster is shared between multiple miles; solid lines indicate that cluster is unique to that trail mile. Thicker lines denote clusters that represent  $\geq 10\%$  of species in that mile.

**Table 1**—Membership of clusters generated from individual species' probability of flowering curves along the route to Mt. Kimball, Santa Catalina Mountains, Arizona, USA.

Cluster	Mile	Cluster membership (count of species)	Cluster membership (% of species in trail mile)	Mean years in flower	St dev years in flower	Annual species	Herbaceous perennial species	Woody species	Succulent species
A	1	205	55.4	6.6	5.5	47%	35%	13%	5%
A	2	202	56.1	5.7	5.6	41%	39%	16%	4%
A	3	185	52.4	6.9	5.9	49%	30%	19%	3%
A	4	159	54.1	6.1	5.7	48%	28%	18%	6%
A	5	112	52.8	6.0	6.0	35%	39%	19%	6%
B	1	15	4.1	26.0	1.5	0%	73%	27%	0%
B	2	13	3.6	26.5	0.8	8%	69%	23%	0%
B	3	17	4.8	26.2	1.7	12%	76%	12%	0%
B	4	12	4.1	26.3	0.9	0%	83%	17%	0%
B	5	5	2.4	26.2	1.1	0%	100%	0%	0%
C	1	32	8.7	24.5	2.2	47%	25%	28%	0%
C	2	18	5.0	25.4	1.8	50%	17%	33%	0%
C	3	33	9.4	22.5	3.3	64%	27%	9%	0%
C	4	22	7.5	20.4	3.8	55%	32%	9%	5%
C	5	4	1.9	24.5	1.0	0%	50%	50%	0%
D	1	26	7.0	22.7	3.2	8%	69%	8%	15%
D	2	41	11.4	24.6	2.9	17%	66%	15%	2%
D	3	39	11.1	25.7	1.4	31%	51%	15%	3%
D	4	23	7.8	25.2	1.9	13%	87%	0%	0%
D	5	16	7.6	25.0	1.9	6%	75%	19%	0%
E	1	34	9.2	18.7	3.7	24%	47%	29%	0%
E	2	36	10.0	21.1	3.6	33%	39%	28%	0%
E	3	51	14.5	20.6	3.9	33%	57%	10%	0%
E	4	48	16.3	18.8	4.0	40%	52%	8%	0%
E	5	31	14.6	20.6	3.7	32%	65%	3%	0%
F	1	41	11.1	18.2	4.1	76%	15%	10%	0%
F	2	41	11.4	20.3	3.7	76%	17%	7%	0%
G	3	13	3.7	24.5	4.5	8%	46%	46%	0%
G	4	16	5.4	24.2	4.3	6%	69%	25%	0%
G	5	9	4.3	25.1	1.5	0%	67%	33%	0%
H	2	9	2.5	25.4	1.1	0%	11%	33%	56%
H	3	15	4.3	23.8	2.9	0%	13%	27%	60%
H	4	14	4.8	23.5	2.9	7%	36%	21%	36%
I	1	17	4.6	23.8	2.9	6%	35%	35%	24%
J	5	35	16.5	16.2	4.4	26%	51%	9%	14%

and narrower in the summer, particularly in the higher elevation miles (4 and 5). Membership of several of the clusters in each mile was quite small (5% or less of the species observed in that mile; fig. 2 and table 1). The distinct flowering patterns exhibited by the species in these clusters are what drive these clusters to exist.

Clusters tended to be dominated by one plant functional type or comprised of a consistent mix of functional types across the elevation gradient (table 1). Cluster B, the bimodal flowering pattern, was comprised of between 73% and 100% herbaceous perennial species (table 1). Cluster C, the spring flowering cluster seen across all 5 miles,

was a mix of annual and perennial species and exhibited a probability of flowering around 60% in miles 1-3; in contrast, the earliest spring flowering cluster exhibited lower probability of flowering, between 40-50% (miles 1 and 2; Cluster F), and was comprised of >75% annual species (table 1). Cluster A, seen in all miles, was a mix of annual and herbaceous perennial species.

For clusters identified in multiple miles, spring cluster peaks generally occurred later at higher miles (fig. 2). The peak for cluster B occurred as a plateau between April 13 and April 27 in mile 1 and peaked around May 19 in mile 5. Summer peaks generally did not

show a lag with increasing elevation. For example, cluster B peaked around September 2 in mile 1 and August 30 in mile 5 in the summer. Similarly, the peak for cluster D was approximately August 30 across all trail miles.

## Discussion

The large membership in cluster A characterizes the great variability in which species flower from year to year in the Sonoran Desert and Sky Islands ecosystems; this analysis reveals that greater than half of the species in each trail mile exhibit a smaller than 10% chance of flowering in any given year or on any particular day. The species in this cluster appear to exemplify the opportunistic nature of many desert plants that are known or expected to depend heavily on seasonal moisture and particular antecedent climate conditions to trigger and complete germination, growth, and flowering (Beatley 1974; Bowers 1987; Bowers and Dimmitt 1994; Kemp 1983). This cluster is comprised of a mix of annual plants, herbaceous perennials, and woody species, which employ different strategies for dealing with variable moisture conditions. As the species in this cluster exhibit very low probability of flowering throughout the entire year and from year to year, these species probably represent a wide range of various antecedent and interacting conditions that cue and sustain flowering.

Aside from the dominant pattern of pronounced year-to-year variability captured in cluster A, there are small “core” groups of species that are consistently seen in flower, similar to the model in figure 1a, regardless of the preceding or concurrent climate conditions. The flowering reliability of these “core” groups increases with increasing elevation, and is also higher in summer than in the spring season. The higher probabilities observed in flowering in summer-season species can be explained by these species’ reliance on the summer monsoon to initiate flowering. Compared to winter and spring precipitation, the onset of the summer monsoon is rather regular in this region, and many species’ flowering cues are closely tied to this seasonal rainfall (Crimmins and others 2011).

The results of this analysis demonstrate clear patterns among functional types that are nested within the broad bimodal flowering patterns characteristic of the Sonoran Desert. At lower elevations, the spring season is characterized by multiple overlapping waves of flowering. The first of these waves is characterized primarily by annual species, though the chances of these species flowering are around 50%. At higher elevations, the spring season is characterized by a mix of life forms and a very small number of species flowering.

At low elevations, the probability of species flowering increases as spring progresses, as does the relative proportion of species in flower that are perennial. Similarly, there are patterns within the summer flowering season that vary by functional types composition, though the timing of these peaks exhibits less temporal variability than the spring season.

Our results show a progressively later spring flowering peak with increasing elevation, consistent with studies in high elevation environments, which have demonstrated a lag in the onset of flowering with increasing elevation where temperature is the most influential variable (Rusch 1993; Ziello and others 2009). Indeed, spring flowering of species in this study area has been shown to be heavily influenced by temperature variables (Crimmins and others 2010). In contrast, we did not see a lag in peak flowering dates with increasing elevation in the summer season. This pattern may be a result of the water limitation in this system. Crimmins and others (2011) showed that across this elevation gradient, the onset of summer flowering is driven by the commencement of the summer monsoon rains and that, especially

in dry years, onset of summer flowering occurs rather synchronously across the plant communities occupying the five trail miles.

The results of this study have value for informing long-term monitoring. Recognizing the low probability of flowering for greater than half of the species present in this system in a particular year could significantly benefit monitoring by informing sampling time frames and/or species selection. Further, if monitoring goals necessitate selection of either consistently or infrequently flowering species, this clustering approach could provide guidance.

The findings of this analysis serve to increase our understanding of the seasonal and year-to-year patterns in plant flowering across this elevation gradient, establishing a critical baseline for comparison under future climate conditions. Recent studies in temperate environments have shown varying sensitivity to climate, with earlier-flowering species advancing their flowering dates at a more rapid pace than later-flowering species (Miller-Rushing and Inouye 2009; Sherry and others 2007). Future research in this unique, water-limited system, where species are adapted to high climate variability, should explore whether this pattern can be expected to manifest here as well. Implications of shifts include opening niches for potential invasion by non-native species and de-coupling of trophic interactions.

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