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Turnover and reliability of flower communities in extreme environments: Insights from long-term phenology data sets

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ABSTRACT

We used three long-term data sets from the southwestern US to investigate the reliability of flowering communities from the perspective of pollinators in extreme environments. The data sets come from three desert sites in New Mexico, two subalpine sites in Colorado, and an elevation gradient in Arizona. We used two indices to explore different temporal scales. We calculated turnover rates of species in bloom on a seasonal basis to investigate how flowering communities change from year to year. We calculated frequency of bloom in the same month over all years to determine the reliability of flowering communities in a narrow time scale. We hypothesized that communities with less reliable precipitation would have lower frequency of bloom and higher turnover rates and that annual plants would show this pattern more strongly than perennials. Flower frequency ranged from 50.3% at the highest elevation AZ site to 66.3% at a subalpine CO site. Within each site, annuals exhibited lower frequencies than perennials. On a seasonal scale, turnover rates ranged from 22.5% in Colorado to 71.4% at a NM site. Looking at the entire flower community as a resource for foraging pollinators, we found that flowers are an unreliable resource, especially in unpredictable environments.

1. Introduction

Flowering phenology plays an important role in the structuring of plant communities as well as the consumers that depend on them. These community-level patterns are affected by their component plant species which have different levels of flowering reliability. Plant phenology studies have long sought to discern which environmental cues yield observed phenological patterns of various individual plant species (Abd El-Ghani, 1997; Adondakis and Venable, 2004; Berlin et al., 2000; Bowers, 1987; Bowers and Dimmitt, 1994; Friedel et al., 1993, 1994; Lambert et al., 2010; Miller-Rushing and Primack, 2008; Pavon and Biones, 2001), related species (Miller-Rushing and Inouye, 2009), or all species in a community (Beatley, 1974; Crimmins et al., 2010; Kemp, 1983).

Plants are sometimes constrained by their phylogeny or evolutionary history (Franks et al., 2007; Kochmer and Handel, 1986; Willis et al., 2008), but many species also exhibit flexibility in their life history to survive climate fluctuations (Willis et al., 2010). At the community level, no two species of plants (Beatley, 1974), not even congeners (Miller-Rushing and Inouye, 2009), respond identically to the array of environmental cues. At the population level, there is a wide range of individual responses, most likely due to a combination of microclimate variability, genetic variation and phenotypic plasticity. All of these factors come together to make the flowering community apparently stochastic from year to year, especially where environmental conditions fluctuate markedly such as in deserts and subalpine areas (Holway and Ward, 1963; Huelber et al., 2006; Kudo and Hirao, 2006). The projected increase in climate variability in the southwest (Overpeck and Udall, 2010; Sheppard et al., 2002) may result in increased variability in phenology in the future.

Few phenology studies look at all species in a community and only a handful of studies have examined the community of flowers from a resource availability perspective (Alarcón et al., 2008;

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Aldridge et al., 2011; Anderson and Schelfhout, 1980; Dupont et al., 2009; Moldenke, 1975; Petanidou et al., 2008; Rabinowitz et al., 1981). Most that do are often only a few years in duration. Our study utilizes three long-term flower phenology datasets from the Sevilleta National Wildlife Refuge in the Chihuahuan desert of New Mexico (9 years), an elevation gradient in the Sonoran Desert outside of Tucson, Arizona (20 years), and a subalpine area at the Rocky Mountain Biological Laboratory in Gothic, Colorado (34 years). These data offer novel insights into long-term reliability of flower communities. In addition, the majority of published phenological studies focus on temperate areas in which temperature dictates phenology. In contrast, arid and semi-arid systems are typically driven by precipitation, not temperature. Phenological studies in these precipitation driven systems are few (Primack and Miller-Rushing, 2011).

To investigate these disparate communities from a resource perspective, we determined the proportion of years that flowering species were available for pollinators in any particular month, averaged across all species in a community and separately for annuals and perennials. In other words, how reliable are the flowers, within a particular community, at a monthly resolution? We also analyzed the data seasonally. For a particular season, what are the chances that a species will flower the following year? We used turnover rates to address reliability of flowering resources from one season to the next. We hypothesized that the sites with the highest variation in precipitation would have the highest turnover of flowers and the lowest frequency of bloom. We also hypothesized that annuals would be less reliable than perennials because they cannot store resources from one season to the next.

2. Materials and methods

2.1. Study locations and data collection

2.1.1. Study location 1, New Mexico

The Sevilleta National Wildlife Refuge is located at the northern tip of the Chihuahuan Desert about 80 km south of Albuquerque in central New Mexico, USA. The refuge lies across an ecotone between Chihuahuan Desert and semi-arid shortgrass steppe. Three sites, representing different ecosystem types were sampled by the Sevilleta Long-Term Ecological Research Program field crew over nine years; Chihuahuan desert black grama grassland (NM-G) dominated by *Bouteloua eriopoda* (elev. 1616 m), Chihuahuan desert creosotebush scrubland (NM-C) dominated by *Larrea tridentate* (elev. 1615 m), and blue grama grassland (NM-B) dominated by *Bouteloua gracilis* (elev. 1670 m).

Data collection: Plant phenology transects were established at black grama and creosotebush sites (NM-G and NM-C) in April of 2000 and at the blue grama site (NM-B) in April of 2001. Data through 2008 were available. There are four replicates (200 × 2 m transects) in each site (1600 m^2 per site). Data were collected monthly from February through October by walking each transect from the north to the south end and recording the phenological status of the first ten individuals of each species. If the first ten individuals recorded were non-reproductive but a reproductive individual was encountered elsewhere on the transect, one of the ten observations for that species was changed to reflect this. So, although not every individual was recorded, all species and all phenology stages were captured in the data. Because these are monthly data, both buds and flowers were considered to be flowering as some plants have short cycles and would be missed if buds were not included. Species identifications were made or confirmed with the aid of the Museum of Southwestern Biology at the University of New Mexico. Data are available online (Wright, 2010).

2.1.2. Study location 2, Arizona

The Arizona study location is composed of the Finger Rock Canyon drainage on the south slope of Mount Kimball in the Santa Catalina Mountains of the Coronado National Forest outside of Tucson, AZ. The base of the trail lies in desert scrub characterized by *Carnegiea gigantea* and *Parkinsonia* spp. at an elevation of 945 m and climbs to pine forest comprised of *Pinus ponderosa* and *Quercus* spp. at an elevation of 2213 m. The elevation gradient was split into five 1.6 km sections with section 1 being the lowest elevation and section 5 being the highest elevation. Each 1.6 km section is considered a site (AZ-1 to AZ-5). The flower assemblages at each site have been shown to be distinct communities by non-metric multi-dimensional scaling ordinations (Crimmins et al., 2008).

Data collection: Phenology data were collected on 1024 roundtrip hikes by David Bertelsen, from 1984 to 2003. The number of hikes per month varied over the study, but each month was represented by at least one hike. Flowering data were collected at the species level for plants visible from the trail. Species identifications were made or confirmed at the University of Arizona Herbarium.

2.1.3. Study location 3, Colorado

Plant phenology data have been collected by David Inouye in several different habitat types since 1973 at the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA. Data from two sites, the Rocky Meadow (CO-RM) and Wet Meadow (CO-WM), were used for this analysis. The Rocky Meadow site (elev. 2966 m) has a relatively early snowmelt period each year. Seven plots were located as close together as one meter, but extend over a distance of 272 m. Vegetative cover is sparse, and most of the species in those plots are different from those at the Wet Meadow site. The Wet Meadow plots are about 100 m lower in altitude, with a relatively late snowmelt period. They are as far apart as 235 m, relatively mesic, and typically have little exposed ground due to the extensive vegetative cover. They are generally more species-rich than the Rocky Meadow plots.

Data collection: Seven and five, 2 × 2 m plots were established at the Rocky Meadow (RM) site and the Wet Meadow (WM) site, respectively. Data were not collected in 1978 and 1990. Flowering data were collected in each plot, every other day for the duration of the growing season (typically May through September).

2.2. Site summary

Table 1 summarizes all the data sets used in this study. Long-term precipitation data (>100 years) were obtained from http://www.wrcc.dri.edu/coopmap/ for the nearest long-term weather station. Mean annual precipitation as well as the coefficient of variation (CV) are reported.

2.3. Data analysis

Because we are mostly interested in animal-pollinated plants, we removed all known wind-pollinated plants as well as obligate selfing plants from the analysis. This yielded 393 species of putative animal-pollinated plants at the Arizona study, 109 in New Mexico, and 71 in Colorado.

Because of considerable differences in experimental design, with total area sampled differing by orders of magnitude and the duration of each study differing significantly, we converted each data set to presence–absence data. This type of data limits inferences on abundance and density, however we believe that comparisons using presence–absence data offer valuable insight into the reliability of flowering communities. Because both turnover rates and frequencies are based on presence–absence data of each species in the community, they represent changes in