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A phenological mid-domain effect in flowering diversity

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Abstract In this paper, we test the mid-domain hypothesis as an explanation for observed patterns of flowering diversity in two sub-alpine communities of insect-pollinated plants. Observed species richness patterns showed an early-season increase in richness, a mid-season peak, and a late-season decrease. We show that a “mid-domain” null model can qualitatively match this pattern of flowering species richness, with R^2 values typically greater than 60%. We find significant or marginally significant departures from expected patterns of diversity for only 3 out of 12 year-site combinations. On the other hand, we do find a consistent pattern of departure when comparing observed versus null-model predicted flowering diversity averaged across years. Our results therefore support the hypothesis that ecological factors shape patterns of flowering phenology, but that the strength or nature of these environmental forcings may differ between years or the two habitats we studied, or may depend on species-specific characteristics of these plant communities. We conclude that mid-domain null models provide an important baseline from which to test departure of expected patterns of flowering diversity across temporal domains. Geometric constraints should be included first in the list of factors that drive seasonal patterns of flowering diversity.

Keywords Flowering phenology · Flowering species richness · Null models · Rocky Mountain Biological Laboratory

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Introduction

Flowering is an important aspect of the life history of angiosperm species, with both ecological and evolutionary consequences. The seasonal timing, or phenology, of flowering is one dimension of flowering that has implications for plant–animal interactions such as herbivory, pollination, and seed predation, and for the potential consequences of environmental events such as late spring or early fall frost (Inouye 2000). Within communities of flowering plants there is the potential for inter- as well as intra-specific competition for resources such as pollinators, or the possibility of interspecific interactions among species sharing floral herbivores or seed predators.

Previous studies have examined the degree of overlap in seasonal flowering of sympatric species to distinguish between aggregation and displacement of flowering periods. Hypotheses that attempt to explain these patterns of flowering phenology include competition for and availability of pollinators and seed dispersers, interspecific facilitation, energy-related or phylogenetic constraints, selection for reproductive isolation (decreased hybrid fitness), and decreased interspecific pollen transfer (Waser 1978; Rathcke and Lacey 1985; Rathcke 1988). In practice, distinguishing among phenological aggregation, displacement, and random assemblage requires an appropriate null model to which observations may be compared (Cole 1981; Rathcke and Lacey 1985; Pleasants et al. 1990; Gotelli and Graves 1996).

Although the degree of phenological overlap in flowering periods has been studied extensively (e.g. Fleming and Partridge 1984), we have not encountered any studies that try to explain the phenological pattern of flowering diversity (Colwell and Lees 2000). This is despite the fact that null models used to assess the degree of phenological overlap are in implementation analogous to null models that have been suggested recently for considering latitudinal gradients in species diversity (Colwell and Lees 2000). Notably, in regions with distinct flowering seasons, fewer species tend to flower near the temporal boundaries of the flowering season than do

toward the middle. Recent work has shown that geometric constraints in random placement of species' ranges (or analogously, flowering period duration) along a defined domain (spatial or temporal) can generate such a parabolic-type gradient in diversity (Colwell and Hurtt 1994; Willig and Lyons 1998; Lees et al. 1999; Colwell and Lees 2000; Jetz and Rahbek 2001, 2002). This pattern has been termed the mid-domain effect.

The mid-domain effect is a generated peak in richness at the mid-point of a bounded n -dimensional domain and was originally described by Colwell and Hurtt (1994) in the context of a latitudinal gradient in diversity (and associated Rapoport effect, i.e., an equatorward decrease in species range). The mid-domain concept can also be applied to a one-dimensional temporal gradient, where randomly placed flowering periods (i.e. temporal ranges—note that in this paper we will refer to the duration of a species' flowering period as its range to remain consistent with previously accepted terminology) will tend to overlap most frequently at the mid-domain, in this case, the middle of the growing season. Geometric boundaries that constrain spatial gradients are replaced in the temporal models by biological boundaries that constrain the temporal domain. For example, at high altitudes the growing season and flowering cannot begin until the snow melts. Constraints on flowering at the beginning of the growing season could include the time necessary to develop buds, and the probability of damage from late snow or frost (Inouye et al. 2002). The end of the season is also determined by the beginning of the next winter's snow cover and cold temperatures. Constraints on flowering at the end of the season include the time necessary to ripen fruits and the danger of frost damage.

As noted previously, models that randomize range placement are not new in the phenological literature. For example, Cole (1981) presented a null model to analyze pairwise overlap in flowering period based on the random placement of flowering periods in the flowering season domain. However, whereas various authors have explored these range-randomization models to assess phenological overlap, or to assess diversity gradients across a spatial domain (e.g. Colwell and Hurtt 1994; Willig and Lyons 1998; Lees et al. 1999; Colwell and Lees 2000; Jetz and Rahbek 2001, 2002), these models have not been used previously to evaluate diversity gradients across a temporal domain (see Colwell and Lees 2000).

One advantage of comparing phenological data against a mid-domain model lies in its flexibility. A researcher may consider dozens of species in an entire community simultaneously, break the community down into functional guilds or taxonomic groups, or even examine single-species flowering curves. Furthermore, each year represents a quasi-independent realization of underlying stochastic processes (e.g. weather-related effects on phenology, irregular abundance fluctuations, pollinator availability), thus we can search for consistency in departure from the model across years in factors that correlate with richness patterns within years. The fact that the beginning of the flowering season in our study site can vary by as

much as almost 6 weeks among years emphasizes the value of a long-term study that can encompass this variation.

In this paper, we test the mid-domain hypothesis against flowering phenology data collected over 7 years in Rocky Mountain sub-alpine meadows and relate these results to possible environmental predictors.

Materials and methods

Data collection

Data used for analyses in this paper were collected by David Inouye at the Rocky Mountain Biological Laboratory in Colorado. Flowering phenology was recorded through counts made every other day for most or all of the growing season for all species occurring in 2×2 m plots. Plots were established in 1973, and have been monitored most years since then. Data for this study came from seven "Rocky Meadow" (RM) plots with shallow soil and relatively sparse herbaceous vegetation, and nine "Wet Meadow" (WM) plots with deep soil and relatively dense herbaceous vegetation. Plots contained representative species from the sub-alpine communities of the Western Slope of Colorado, generally dominated by long-lived perennial forbs. We limited our study to insect-pollinated forbs (excluding several species of grasses, a few sedges, and a few other species). The seven RM plots (six of them in the same small meadow) ranged in altitude from 2,941 to 2,988 m (latitude 38°57.745–605'N, longitude 106°59.135–213'W) and the nine WM plots (all in the same large meadow) were all at about 2,886 m (latitude 38°57.336–770'N, longitude 106°59.212–276'W). The distance between the two closest RM and WM plots is about 500 m, and the most distant RM and WM plots are separated by about 900 m. The RM plots, some of which are on south-facing exposures, melt out earlier in the spring and dry out earlier in the summer than the WM plots, which are all on level ground. The plots have experienced little human induced disturbance since the early 1900s and are subject to little vertebrate grazing and browsing (cattle have been excluded since 1987, but deer and probably bear and elk sometimes eat plants in the plots).

Six years (1995, 1996, 1998–2001—the most recent for which data have been processed) were selected to explore year-to-year variation in the fit of the null models. Results are presented graphically for 1995, 1999, and 2001—comprising an exceptionally early, intermediate, and exceptionally late starting dates of the flowering seasons.

Because of the sampling regime (approximately every other day), the first or last dates of flowering may have been underestimated by a day. Consequently, the flowering period for a species was calculated using estimated first and last dates of flowering. For example, the first date of flowering was estimated by taking the midpoint of the first date a species could have flowered (i.e., 1 day after the last census in which no flowering was observed) and

the first date a species was observed to flower. A similar approach was used to estimate the last date of flowering. Typically, this resulted in an adjustment of one day for the flowering period. The flowering season was defined by the first flower of any species to the last flower of any species. Snowmelt and the first flowering can occur between mid April and early June at this study site, and flowering is mostly finished by mid- to late August, although occasional flowers have been recorded into late September or even October.

Model selection

A variety of null models has been proposed to test predictions of the mid-domain effect. These include both range- and midpoint-constrained models and fully stochastic models that generate theoretical range-size frequency distributions (Colwell et al. 2004). It is important to emphasize that the interpretation of these null-model analyses is relative to the underlying assumptions of each model. For example, it would be possible to generate predictions of flowering diversity assuming an unbounded temporal domain—that is, flowering is equally likely throughout the year. Obviously, such a null model would be rejected, and we would conclude from rejecting this null model that flowering is significantly clumped seasonally with lower than expected flowering during that part of the year with expected temperatures below freezing. Thus, deviations in observed flowering diversity from expectations based on a fully stochastic model indicate that departures in either or both the distribution of ranges and midpoints drive this difference. Similarly, analysis of a midpoint- or range-constrained null model allow us to assess the effects of departures in either the distribution of midpoints or ranges, respectively. For our analysis, we chose to use a null model constrained by the empirical ranges of the flowering periods. This is equivalent to asking: “given the distribution of flowering ranges in our data set, what is the expected pattern of flowering diversity over time?” For a more complete review of the different null models, and a discussion of why a range-constrained null model analysis is preferred for the analysis of empirical mid-domain effects, see Colwell et al. (2004).

Application of the model to a temporal domain is a simple process, but one that merits explanation. Consider a flowering season (the domain) of n days. To use a mid-domain null model to investigate the temporal patterning of flowering richness, we reduce the occurrence of each species’ observed flowering period to two parameters—its midpoint and duration. We then “reshuffle” the observed ranges in the domain (by resampling with replacement) so that each range is assigned a new random midpoint given the constraint of possible midpoints imposed by length of the flowering period. For a flowering duration that extends n days (begins flowering on the first day of the season and ends on the final day) there is only one possible midpoint (at day $n/2$) whereas a flowering period of 3 days will

have $n-2$ possible midpoints (the only 2 days that cannot be selected as a midpoint would be days 1 and n). This process is repeated for each species in the community to create a random flowering richness curve. Note that in our simulations we used a half-day interval to accommodate estimated flowering periods that included half-days.

Statistical analysis

Testing data against the mid-domain model to explore null model fit within years presents obvious challenges. One can easily determine how much of the variation in species richness across the flowering season is captured by the model (e.g. linear regression), but actually testing for departure from the model is more complex. If the model explains 95% of the variation in number of flowering species throughout the flowering season, we still do not gain any insight into the degree of “randomness” of richness patterns. To explore null model fit within years, we assessed the degree of departure of these models using a simulation approach advocated by Veech (2000). We began by simulating the null model 20,000 times. We used these simulations to generate the expected seasonal pattern of flowering diversity, calculated as the mean daily diversity from day 1 to n based on all 20,000 simulations. For each simulation, we calculated the mean displacement (*MD*) as the absolute value of the difference between the simulated diversity and the observed diversity for each census date averaged over the season (Veech 2000). We repeated this procedure for each of the 20,000 simulated data sets to generate a probability distribution for this test statistic. Finally, we determined the *MD* value for the observed data set as above and compared it to the generated probability distribution to calculate a *P*-value. Veech (2000) showed that this approach has high power for detecting deviations from randomness for communities with greater than 20 species and for data sets with greater than ten sampling periods, as in our analyses.

To examine whether communities showed consistent departures from the null model across years, we divided the domain into 75 equally spaced time periods (effectively standardizing the richness patterns to a season of 75 days) and compared estimated to simulation-predicted richness. We chose 75 with the goals of maximizing residuals sampled, and because no year had a flowering season that lasted less than 75 days. These residuals were compared across years.

A final issue with testing null models based on random placement of flowering periods (or species’ ranges in general) is that the simulated season length (i.e. domain) will typically be less than the observed season length (Ashton et al. 1988). Recall, we defined the onset of the observed flowering season as the date of first flower. The earliest flowering date of the simulated data set can only be equal to or later than the observed first date of flowering, and the latest flowering date of the simulated data set can only be equal to or earlier than the observed last date of flowering. To correct for this, the simulated

season length was increased symmetrically so that the average simulated season length equaled the observed season length (Ashton et al. 1988). The level of adjustment was determined by padding the beginning and end of the season length. Each season length was simulated 100 times, and regression was used to infer the level of adjustment that generated a predicted season length equal to the observed season length. In practice, this adjustment was small—on average less than 2% of the season length, and in no case larger than 5%.

Results

Flowering seasons began from early May to early June, and lasted until mid-September or early October (Table 1). More species flowered in the WM plots than in the RM plots (Table 1). Observed species richness patterns for both the RM and WM plots indicated a tendency for mid-domain peaks across all years (Figs. 1, 2). When flowering season was divided into three equal time periods, observations showed a clear increase in richness over the initial period followed by a peak in richness in the middle period, followed by a gradual decline in richness in the third period. The null model explained a large proportion of the variation of species richness across the temporal gradient for each year of the analysis (Table 2). With respect to the pattern of flowering diversity (*MD*, mean displacement), observed diversity over time in the RM plots was significantly different from the null model predictions only in 1996 (Table 2; Figs. 1, 2). On the other

hand, residuals (observed flowering diversity minus null-model-predicted flowering diversity) from 1996 were highly correlated with 3 out of the 5 years (Table 3). For the WM plots, there was more of a trend towards departure from the null model predictions, but this difference was significant only for 1995 (Table 2; Fig. 1).

For both the RM and WM plots, residuals averaged across years showed significant deviations from predicted diversity (Fig. 3). In the RM plots diversity was lower than expected at the beginning of the season, and higher than expected for the remaining first third of the season (Fig. 3). Flowering diversity in the WM plots also showed strong departures from predicted diversity averaged across years (Fig. 3). However, the pattern of deviation was different than for the RM plots, with diversity significantly lower than predicted for the first half of the season and higher than predicted for the second half (Fig. 3). Both RM and WM plots showed lower than expected flowering diversity over the earliest part of the flowering season.

Discussion

Early tests of the mid-domain effect explored the extent to which null models that include geographic constraints in one dimension could explain latitudinal gradients in diversity (Willig and Lyons 1998; Lees et al. 1999). More recently, tests of the mid-domain effect have expanded to include an analysis of diversity in two dimensions (Jetz and Rahbek 2001; Hawkins and Diniz-Filho 2002). So far, support for the mid-domain effect as a

Table 1 First and last dates of flowering, and number of species flowering (excluding wind-pollinated species) in the RM and WM plots at the Rocky Mountain Biological Laboratory

	Year					
	1995	1996	1998	1999	2000	2001
RM plots						
First observed flower	9 Jun	14 May	9 May	20 May	5 May	7 May
Last observed flower	1 Oct	14 Sep	23 Sep	21 Sep	4 Sep	24 Sep
Domain (days) ^a	118.5	129	145	129	129	147.5
Maximum range (days)	89.5	64	86.5	113.5	68.5	100.5
Number of species ^b	33(18)	35(15)	37(20)	34(16)	34(19)	30(17)
WM plots						
First observed flower	10 Jun	22 May	19 May	23 May	13 May	15 May
Last observed flower	28 Sep	3 Sep	17 Sep	21 Sep	9 Sep	15 Sep
Domain (days) ^a	114	108.5	126	123.5	126	126
Maximum range (days)	61.5	49	90.5	102.5	109	106
Number of species ^b	53(38)	50(30)	51(34)	52(34)	50(35)	48(35)

^a Domain used for simulations

^b Number in parentheses indicates number of species unique to each community for that year

Table 2 R^2 values and mean displacement with associated P -values (*MD*, P -value) for null model analysis within years

Model	Year						Mean \pm SE
	1995	1996	1998	1999	2000	2001	
RM plots							
R^2	0.91	0.61	0.77	0.85	0.64	0.41	0.69 \pm 0.07
<i>MD</i>	1.15, 0.952	2.81, 0.043	1.63, 0.724	1.21, 0.944	1.61, 0.652	1.51, 0.64	1.69 \pm 0.25
WM plots							
R^2	0.65	0.85	0.85	0.88	0.69	0.78	0.78 \pm 0.04
<i>MD</i>	5.21, 0.009	3.18, 0.133	3.89, 0.054	3.32, 0.117	3.15, 0.119	2.85, 0.231	3.6 \pm 0.35

Bold values indicate significance for *MD* values at $P < 0.05$. Note that significance levels are not reported for R^2 values because of the inherent autocorrelation in this data set

Fig. 1 Observed and null-model-predicted flowering diversity over time for RM and WM plots in 1995, 1999, and 2001. 1995 was an exceptionally late year for flowering, 1999 was an average year, and 2001 was an exceptionally early year. Note the frost-associated decline in flowering diversity around mid-June for 2001

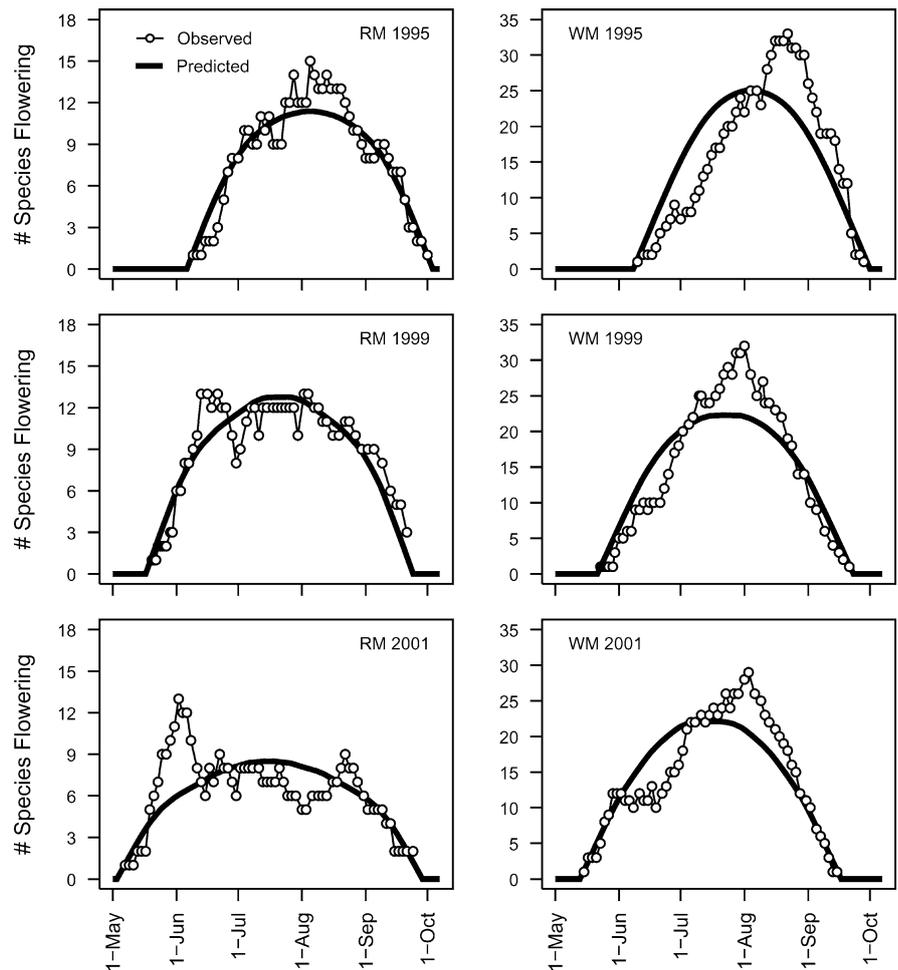


Table 3 Correlation matrix for time-normalized residuals between years within models for RM plots. Note that significance levels are not reported because of the inherent autocorrelation in this data set

	Year					
	1995	1996	1998	1999	2000	2001
1995	1	0.25	0.24	0.04	0.05	-0.26
1996	-	1	0.64	-0.08	0.73	0.17
1998	-	-	1	0.24	0.64	0.5
1999	-	-	-	1	0.19	0.41
2000	-	-	-	-	1	0.28

significant predictor of diversity has been mixed. Although there is a signature of the mid-domain effect in many of the studies that have looked for one (Colwell et al. 2004), the effect of geographic constraints appears to be relatively weak compared to other factors (Jetz and Rahbek 2002).

In this paper, we explore the mid-domain effect in flowering diversity using a mid-domain null model across a temporal domain. This null model of a phenological mid-domain effect explained a large percentage of the temporal variation in flowering diversity, and qualitatively matched the observed mid-season increase. Moreover, we only detected a significant or marginally significant

departure from the null-model predictions in 3 out of 12 year-site combinations. Rather than a null hypothesis of constant flowering diversity over a season, our results support the view that a mid-domain peak in diversity is the appropriate null that should be used for studies testing ecological explanations for seasonal patterns of flowering diversity. Geometric constraints should be included first in the list of factors that drive seasonal patterns of flowering diversity.

Although results from these null model analyses match observed patterns (Table 2, Fig. 1), we do find significant departures from expected patterns of diversity with respect to the observed pattern of diversity (*MD*) in at least some years (Table 2), and a consistent pattern of departure in the residuals averaged across years (Fig. 3, Table 3). Qualitative analysis of these residuals provides an opportunity to test for non-geometric factors that may constrain patterns of flowering at these sites.

Determinants of flowering diversity phenology

Because the null model provided a reasonable representation of the distribution of flowering richness for both the RM and WM plots, we feel justified in its use to assess common environmental factors that may affect patterns of

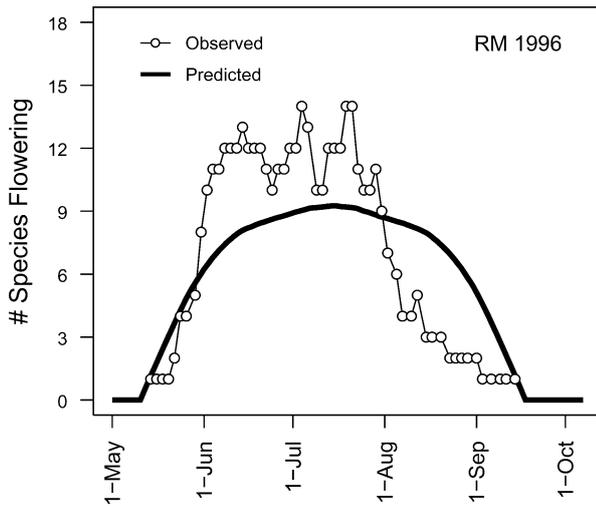


Fig. 2 Observed and null-model-predicted flowering diversity over time for 1996 in the RM plots—the only year of six in which the pattern of flowering. *MD* was significantly different than predicted for this site

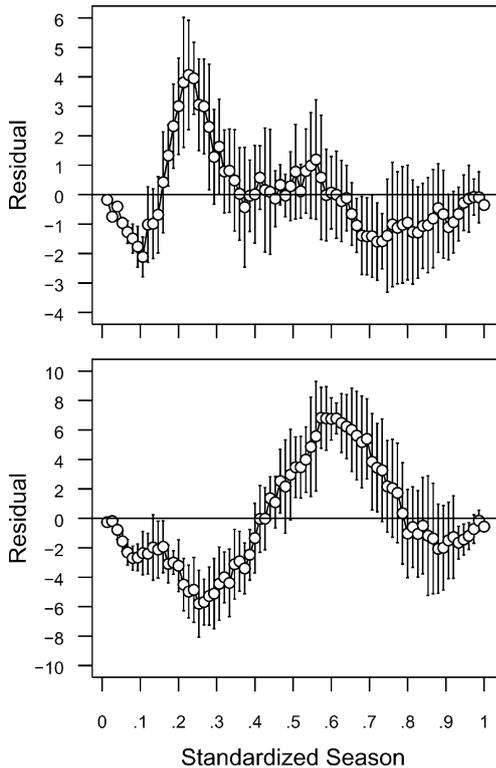


Fig. 3 Average $\pm 95\%$ CI residual from null-model analysis (i.e. observed-null-model-predicted flowering diversity) across years for a standardized season length of 75 days for RM (*top*) and WM (*bottom*) plots

phenological diversity. Despite differences between plots, there are some consistencies that may be attributed to shared climatic factors. For example, although the pattern of deviation from the null model predictions varies between sites, both sites show a similar early-season depression in flowering diversity (Fig. 3). This feature may be an evolutionary outcome of the increased

frequency of early-season frost events, which can have significant impacts on flowering diversity (Inouye 2000; Inouye et al. 2002). The potential impact of such an early season frost event is illustrated in Fig. 1, where an exceptionally early onset of flowering for 2001 was associated with a late season snowfall on 13 June, a frost event on 15 June (the temperature dropped to -5.5°C), and a concomitant decline in flowering diversity.

Similarly, both sites show a general excess in observed flowering diversity relative to expected at some point following this early season trough. One possibility is that this pattern is partially controlled by temperature, since metabolic rates scale with temperature (Gillooly et al. 2001). Furthermore, flowering phenology for some species appears to be in part a function of degree days since snowmelt (D. W. Inouye, unpublished data). Temperature data collected from 1971–2000 at Crested Butte, Colo. (located 9.5 km from RMBL at an elevation of 2,704 m) show that the maximum average temperature occurs between 20 July and 7 August (NCDC 2003). For the WM plots and for years depicted in Fig. 1, maximum observed diversity occurs on 22 August 1995, 1 August 1999, and 2 August 2001. On the other hand, this mid-season peak in diversity for the WM plots is associated with only a weak to non-existent corresponding peak in diversity for the RM plots. Rather, there is an earlier peak in diversity for the RM plots that is not associated with a corresponding peak in diversity for the WM plots. It is possible that this dissimilarity is driven by differences in slope/aspect that might influence microclimate as the RM plots melt out earlier in the spring, or to differences in species composition between sites.

For the WM plots, flowering diversity is significantly different from the null model for 1995 in particular—a year with an exceptionally early onset of flowering (Table 1). Most of the variation in timing of flowering among years is explained by how much snow fell during the previous winter; the more snow, the later flowering occurs (e.g., Inouye and McGuire 1991; Inouye et al. 2002, 2004). On the other hand, the only year that showed significant departures from the null model for the RM plots was 1996—an average year with respect to onset of flowering.

In general, the differences in flowering phenology and diversity between plots outlined in this paper may be due to corresponding differences in species composition, richness, or environment. Average richness in RM plots was 34 species vs. 51 in WM plots, and average percent shared species relative to the total species between plots was 32% (Table 1). Veech (2000) showed that for communities with at least 20 species and ten sampling intervals mean displacement had high power to detect deviations from a mid-domain null model for a community with known structure. This result suggests that a difference in statistical power, per se, is unlikely to drive the differences between plots observed in this study. A more likely explanation is that differences in species composition between sites drive the difference in patterns of flowering diversity. In fact, a few species may have a

disproportionate effect on the deviation in the pattern of flowering diversity relative to expected under the null model because the mid-domain effect is expected to be especially pronounced for species with large ranges (Colwell et al. 2004).

The fact that WM and RM plots show different degrees and patterns of departure from the null model implies that different factors affect the between-year variation in patterns of flowering diversity for these sites. For example, RM plots, due to their more shallow soils, shorter vegetation, and lower percent cover by plants, are probably more susceptible to drought conditions. More studies will be needed to understand the environmental factors that drive these site-specific differences in flowering diversity.

Conclusions

We show that a mid-domain null model can qualitatively match patterns of flowering species richness for each of 6 years in two habitats. We argue that geometric constraints should be included in the list of factors that drive seasonal patterns of flowering diversity.

We also stress that other factors traditionally used to describe patterns in flowering phenology are not challenged here, and in fact, our analyses provide some support for these interpretations. Specifically, we find significant departures from expected patterns of diversity for at least some years and a consistent pattern of departure when comparing observed versus null-model predicted flowering diversity averaged across years. These results suggest that ecological factors do shape patterns of flowering phenology, but that the strength or nature of these environmental forcings may differ between the two habitats we studied or may depend on species-specific characteristics of these plant communities.

Because this paper does not consider applicable subsets of the flower community (e.g. based on taxonomic relatedness or shared specific pollinators), we encourage the study of such comparisons using models that incorporate geometric constraints. Models that incorporate flowering abundance among years might also help to elucidate the significance of environmental variables (e.g., Inouye and McGuire 1991; Inouye et al. 2002; Saavedra et al. 2003). Additionally, we encourage the application of null models for a variety of phenological patterns, including single species and even individual plant flowering patterns.

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