

# Transient patterns in the assembly of vernal pool plant communities

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**Abstract.** Community assembly theory asserts that the contemporary composition of ecological communities may depend critically on events that occur during the formation of the community; a phenomenon termed “historical contingency.” We tested key aspects of this theory using plant communities in over 200 experimentally created vernal pools at a field site in central California, USA. The experiment was initiated in 1999 with construction of vernal pool basins into which different seeding treatments were imposed to evaluate the effects of dispersal limitation, order of colonization (“priority effects”), and frequency of colonization on plant community composition. We tracked the abundance and distribution of five focal species for seven years following seeding and observed strong but transient effects of seeding, as well as order and frequency of colonization. All five species occurred with higher frequency in seeded pools vs. unseeded control pools, demonstrating dispersal limitation. Three of four species exerted strong priority effects, with much higher abundance in pools in which they were seeded first compared to pools in which they were seeded in the second year of the study, one year after other species were seeded. We tested for effects of frequency of colonization using one species, the endangered *Lasthenia conjugens*, and observed much higher abundance in frequently vs. infrequently seeded pools for the first four years following seeding. Finally, we observed that the strength of priority effects varied significantly with water depth for one of the species groups, which demonstrates that abiotic context can strongly influence species interactions. We conclude that several aspects of historical contingency play key roles in the early formation of vernal pool plant communities. But we also observed reversals in community trajectories, suggesting that in this system historical effects may be lost within a decade.

**Key words:** California, USA; community assembly; endangered species; grasslands; *Lasthenia conjugens*; priority effects; restoration; vernal pools.

## INTRODUCTION

Efforts to understand the factors controlling the composition of local communities have played a central role in the development of ecology (Diamond 1975, Strong et al. 1984, Pimm 1991, Weiher and Keddy 1999, Hubbell 2001, Chase 2003, Tilman 2004, Holyoak et al. 2005). Community assembly theory posits a crucial role for historical contingency in community development (Drake 1990, 1991, Lockwood 1997, Belyea and Lancaster 1999), which refers to stochastic events that cause community trajectories to diverge, even under identical environmental conditions. Specifically, the identity of colonists, the order of species colonization, and the frequency of colonization events for a given species may all affect subsequent community development. The extent to which community composition is historically contingent remains a major knowledge gap in ecology, however, because it is typically difficult to observe early stages of community formation (Weiher

and Keddy 1999, Fukami et al. 2005, Young et al. 2005). We used the restoration of native vernal pool plant communities to test hypotheses regarding the relevance of colonization patterns on plant community formation.

### *Theory and observations of community assembly*

Community ecology is rich with theory regarding processes of community assembly and succession (Young et al. 2001, 2005, Suding et al. 2004, Temperton et al. 2004). Succession theory suggests a deterministic route toward a community following disturbance and predicts that communities on similar sites will converge toward a single, stable endpoint. Alternatively, assembly theory suggests that the composition of communities is influenced strongly by historical factors (Drake 1990, Belyea and Lancaster 1999, Chase 2003) and that communities on similar sites may diverge toward multiple, stable endpoints based on events that occur during colonization. For example, there may be “priority effects” if the first species to colonize a habitat is the most likely to persist in that habitat, all else being equal (Drake et al. 1993).

Despite a collection of theoretical models and field studies, we still lack a detailed understanding of how

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natural communities are shaped by historical colonization patterns, in addition to other abiotic and biotic constraints. Investigations of community assembly have been conducted primarily via computer simulations (Law and Morton 1996, Lockwood et al. 1997), in experimental microcosms (Weiher and Keddy 1995, Drake et al. 1996, Jiang and Patel 2008), and in a limited number of field experiments (Fargione et al. 2003, Fukami et al. 2005, Emery and Gross 2006, Irving et al. 2007, Körner et al. 2008). Computer simulation and microcosm studies have generally revealed that communities may reach alternative endpoints ("multiple stable equilibria"), depending critically on events that occur during community formation as well as on environmental characteristics or disturbance regimes (Chase 2003, Jiang and Patel 2008).

The outcome of community assembly trajectories may vary significantly, depending on the position of communities along environmental gradients. We know relatively little about how key factors in community assembly vary with such abiotic contexts. A recent evaluation of research frontiers in ecology (Agrawal et al. 2007) asserted that more work is needed to determine how environmental variation affects interaction strengths across environmental gradients. For example, the community of plant species supported by an ephemeral vernal pool should depend on its depth, because deeper pools hold water longer, excluding more species that can't tolerate inundation. Our long-term study of restored vernal pool plant communities provides an excellent setting to evaluate the relative strength of interactions involved in community assembly across gradients of water depth.

Experiments in ecological restoration present rare opportunities to examine factors that affect the formation, structure, and stability of ecological communities. The goals of restoration ecology are to recover native populations, communities, and ecosystem function in degraded habitats (Jordan et al. 1987, Zedler 2000, Temperton et al. 2004, Falk et al. 2006). Thus, restoration of natural communities can furnish insights into whether community composition is deterministic, following predictable trajectories, or it depends significantly on variation in species arrivals that can drive community trajectories in different directions (Lockwood and Pimm 1999, Young et al. 2005).

#### *Vernal pool plant communities*

Restoration of vernal pool ecosystems, combined with reintroduction of populations and communities, are crucial aspects of vernal pool recovery from widespread habitat destruction. A recent survey concluded that approximately  $1.2 \times 10^6$  ha of vernal pools have been lost in California since European settlement and fewer than  $0.40 \times 10^6$  ha remain (R. F. Holland, *unpublished manuscript*). Vernal pools are seasonal wetlands with abrupt boundaries that form on relatively level sites underlain by an impervious hardpan soil layer (Zedler

1987, Holland and Jain 1988). They are typical of Mediterranean climates (Grillas et al. 2004, Deil 2005) and are characterized by winter and spring inundation of pools, followed by complete drying in summer. California's vernal pools are distinct in that they support a highly endemic and largely annual flora (Holland and Jain 1981). Vernal pools in California become flooded soon after the onset of winter rains, and seedlings establish from seeds produced during the previous spring(s) (Zedler 1987). Seedlings persist underwater during the aquatic phase, typically December to March each year. In March through May, water evaporates from the pools and the predominantly annual plants flower and set seed. Seeds either germinate in response to winter rains in November or remain dormant in the seed bank.

We examined how historical contingencies affect vernal pool plant community composition in the early phase of community formation. Specifically, we manipulated the sequence and timing of species arrivals by initializing different pools with propagules of differing species mixtures to ask whether (1) vernal pool plant species were dispersal limited, (2) the order of species colonization significantly affected plant species composition, (3) the frequency of colonization events affected plant relative abundance, and (4) physical factors influenced the strength of biological interactions among species.

#### METHODS

##### *Study site and focal species*

We conducted this study at Travis Air Force Base (AFB) in Solano County, California, USA. Travis AFB is located in the Sacramento Valley of California, near the town of Fairfield, approximately equidistant from Berkeley and Davis, California ( $38^{\circ}15'00''$  N,  $122^{\circ}00'00''$  W, 6 m elevation). This area receives  $\sim 50$  cm of rain per year, concentrated in the winter wet season from December to April. There is typically no measurable precipitation from May to November. Approximately 100 naturally occurring vernal pools occur in the 15-ha study area, embedded in a grassland matrix recently used for grazing and cultivation agriculture (BioSystems Analysis 1994).

Travis AFB hosts one of few remaining populations of the annual plant *Lasthenia conjugens* (Contra Costa goldfields, Asteraceae: Heliantheae), which is limited to vernal pool environments in central California. Because of habitat loss, *L. conjugens* is listed as an endangered species, and its legally protected status makes it the target of the restoration effort described here. However, the project's ultimate goal is to reconstruct viable vernal pool communities. To this end, we investigated effects of manipulating the abundance of *L. conjugens* as well as four additional species native to vernal pools, including *Eryngium vaseyi* (button celery, Apiaceae), *Deschampsia danthonioides* (annual hairgrass, Poaceae), *Layia chrysanthemoides* (tidy tips, Asteraceae), and *Plagiobothrys*

TABLE 1. Seed addition treatments for experimental pools created at Travis Air Force Base in Solano County, California, USA.

Treatment	Year 1 (1999)	Year 2 (2000)	Year 3 (2001)
Control	no seeds	no seeds	no seeds
<i>L. conjugens</i> 1×	100 seeds	no seeds	no seeds
<i>L. conjugens</i> 3×	100 seeds	100 seeds	100 seeds
Group A priority	100 seeds each of group A species	100 seeds each of group B species	no seeds
Group B priority	100 seeds each of group B species	100 seeds each of group A species	no seeds

Notes: Group A consisted of *Lasthenia conjugens*, *Deschampsia danthonioides*, and *Eryngium vaseyi*. Group B consisted of *Lasthenia conjugens*, *Plagiobothrys stipitatus*, and *Layia chrysanthemoides*. Years indicate the year in which seeds were added to experimental pools. After year 3, no additional seeds were planted, but species composition measurements continued as previously.  $N = 64$  pools for the control and group treatments, and  $N = 32$  for each of the *Lasthenia conjugens* treatments.

*stipitatus* (popcorn flower, Boraginaceae) (Hickman 1993).

#### Design of the field experiment

We collected observational data in 1998 and 1999 on all plant species that occurred in sampling plots in naturally occurring “reference” pools within our study site. These data provided the basis for choosing the five focal species noted above for inclusion in our field experiment. In reference pools, *D. danthonioides*, *E. vaseyi*, and *Lasthenia conjugens* had relatively high local densities (mean frequency = 40%, 47%, and 48%, respectively, measured as the number of subquadrats in which the species occurred out of 100 in a 0.25-m<sup>2</sup> sampling quadrat;  $N = 20$  pools in 1999). *Plagiobothrys stipitatus* and *Layia chrysanthemoides* also occurred in reference pools but generally had lower local densities (mean frequency = 15% and 5%, respectively) than the other three species.

The reference pools at our study site line a minor landing strip in the northwest corner of Travis AFB. In December 1999, we constructed 256 “experimental” pools in a regular grid bisected by this landing strip. Experimental pools had the same soils as reference pools (Antioch San Ysidro complex and San Ysidro sandy loam), were similar in elevation, had relatively level topography (0–2% slopes), likely supported vernal pools historically, and were in close proximity to reference pools. Experimental pools were designed to mimic reference pools in five physical dimensions (S. K. Collinge and J. T. Marty, *unpublished manuscript*): (1) size, (2) shape, (3) slope, (4) maximum depth, and (5) topography of intervening grassland habitat. Among these variables, only size was varied. Within a regular matrix of pool positions, each position was assigned a pool size at random: large (5 × 20 m), medium (5 × 10 m), or small (5 × 5 m). Experimental pools range in distance from 15 to 150 m from reference pools, and each pool is 10 m from the nearest experimental pool, a typical distance between reference pools at this study site. Vernal pool plant species typically have limited dispersal abilities (Zedler 1990, Spencer and Rieseberg 1998), so the scale of our design is appropriate for exploring how early colonization events shape these plant communities. Effects of pool size and spatial context on community dynamics within and among

pools, metacommunity dynamics, will be addressed in detail in a subsequent publication. The current analysis provides mean field results relevant to some of the many nonspatial models that contribute to the theoretical foundation of community ecology.

We collected seeds of the five focal species from reference pools during May and June of 1999, 2000, and 2001, for inoculation of experimental pools. Counted seeds were stored in coin envelopes under cool, dry conditions and were planted within one year of collection to maximize seed viability. To ensure representation of genetic diversity from reference pools, we selected seeds of each species for each experimental pool from 10 different individuals (10 seeds × 10 individuals = 100 seeds per species per pool). We confirmed that this protocol was effective in capturing and distributing genetic diversity by examining subsequent generations of *Lasthenia conjugens*: populations in reference and experimental pools maintained equally high levels of genetic diversity (Ramp et al. 2006). In early December of 1999, 2000, and 2001, prior to winter rains, we distributed seeds according to the four seed addition treatments (Table 1). Seeds were distributed within permanently marked, 0.5 × 0.5 m plots (one plot per experimental pool). Plots in each pool were located where we expected water depths of 5–10 cm during inundation, to control for effects of varying water depth on plant performance.

Seed addition treatments were randomly assigned among pools. To prepare plots for initial seeding, we lightly raked the 0.25 m<sup>2</sup> area of the seed plot. In years 2 and 3, we did not rake the plots since this may have disturbed seeds from previous years. Seeds were combined with a scant tablespoon of fine sand and scattered over the soil surface. Pools in the unseeded control treatment were similarly raked and sprinkled with fine sand. We chose inoculations of 100 seeds for the *L. conjugens* treatment and 100 seeds of each species for the group treatments (Table 1), to mimic initial natural colonization of vernal pools, which would likely involve a relatively small number of propagules.

#### Field data collection

Because seasonal inundation is a defining property of vernal pools, we characterized winter flooding of pools at the study site during two wet seasons. Limited

financial resources precluded measurements in additional years of the study. At weekly intervals during the wet seasons of 1999–2000 and 2001–2002, we recorded standing water in all experimental pools ( $N = 256$  pools) and in a subset of the reference pools ( $N = 31$ – $32$  pools) for 10–15 weeks. We calculated the duration of inundation (number of days inundated) for each pool and recorded the depth of water at the center of each pool, as well as at the center of vegetation sampling quadrats in each pool. In experimental pools, our sampling quadrats were the seed plots, where maximum water depths were expected to be 5–10 cm. In reference pools, we placed one to three sampling quadrats haphazardly in locations where water depths were also expected to be 5–10 cm, to facilitate comparison between experimental and reference pools.

We measured plant occurrence in experimental pools during the flowering phase (April–May) each year from 2000 to 2008. We placed a square frame ( $0.50 \times 0.50$  m =  $0.25$  m<sup>2</sup>) divided into 100 subquadrats (each  $5 \times 5$  cm) over the marked plot in each pool and recorded the number of individuals of each of the five focal species (Table 1), as well as the frequency (number of subquadrats out of 100 in which the species occurred) of all species present within each marked plot in each year. Plants were identified to species using Hickman (1993), and a voucher collection is maintained in the Collinge laboratory at the University of Colorado at Boulder.

#### Data analyses

We characterized the outcomes of different seeding treatments in several ways. To evaluate the effects of seeding (“dispersal limitation”) we compared the summed frequencies of the five focal species in seeded pools vs. control pools for seven years following the final seeding treatments (2002–2008). We calculated the magnitude of a priority effect as the mean frequency of each species in pools in which it was seeded in 1999 minus its mean frequency in pools in which it was seeded in 2000 (see Table 1 for seeding timetables). For example, the priority effect for *D. danthonioides*, a species in group A (see Table 1 for definitions), was calculated as its mean frequency in group A priority pools minus its mean frequency in group B priority pools for each sampling year (2002–2008). We examined whether the strength of the priority effect varied with pool depth by plotting the mean priority effect vs. the maximum water depth measured in the pool during the 1999–2000 wet season. We expected that priority effects would be maximized either in pools of intermediate depth or in the deepest pools. Therefore, we compared the null model (no variation with depth) with a quadratic model (peaking at an intermediate depth) and a saturating model (rising asymptotically with depth). To compare support for these non-nested models, we used corrected Akaike information criterion (AIC<sub>c</sub>), which discounts model likelihood by the number of model parameters, and, unlike the likelihood ratio, is

appropriate for ranking non-nested models (Burnham and Anderson 2002). Following Burnham and Anderson (2002), we assumed that the model with the smaller AIC<sub>c</sub> was much better supported by the data if the difference in AIC<sub>c</sub> values was more than four units. We evaluated the effect of the frequency of colonization attempts by *L. conjugens* by comparing the frequency of this species in pools in which it was seeded in three consecutive years to those in which it was seeded only once. To characterize the size of the effect of seeding on the frequency of focal species, we generated a confidence interval on the mean difference between summed frequencies of focal species in seeded vs. control pools using the Welch’s two-sample *t* test, which allows for unequal variances. Analyses and plots were coded in R 2.6.2 (R Foundation for Statistical Computing, Vienna, Austria).

#### RESULTS

Importantly, the hydrological function of experimental pools was similar to that of reference pools. To summarize results presented elsewhere (S. K. Collinge and J. T. Marty, *unpublished manuscript*), both types of pool held standing water for ~10 weeks in 1999–2000 and for 15 weeks in 2001–2002. The average depths of reference and experimental pools did not differ significantly except during the first few weeks of the wet season of 2001–2002, when reference pools were slightly deeper. Despite annual differences in precipitation, maximum water depth and duration of inundation were significantly, positively correlated between years in both experimental and reference pools. In the current analysis of experimental pools, we found no differences among the seeding treatments in maximum depth of water or duration of inundation in either wet season (data not shown).

#### Seeded vs. control pools

When combined, the five focal species had much higher frequencies in seeded pools than in control pools for six of the seven years following the final seeding treatments (Fig. 1). As late as 2007, the summed frequencies of focal species in seeded pools was significantly higher than in control pools ( $81.04 \pm 63.06$  in seeded pools,  $39.07 \pm 39.94$  in control pools [mean  $\pm$  SD]). A 95% confidence interval for the effect of seeding on the summed frequencies of focal species was 23.98–60.94, meaning that focal species occurred with at least 24% higher frequency in seeded pools. The effect of seeding waned over time as control pools were gradually colonized by focal species and as the frequency of focal species declined in seeded pools. In 2006 and especially in 2008 the frequency of focal species dropped substantially in seeded pools. By 2008, the difference between seeded ( $28.52 \pm 35.61$ ) and control pools ( $17.39 \pm 20.49$ ) remained barely significant (a 95% confidence interval for this difference was 3.77–18.49); the strong effect of seeding had been lost.

The loss of species from seeded pools was more substantial than the gain through colonization of

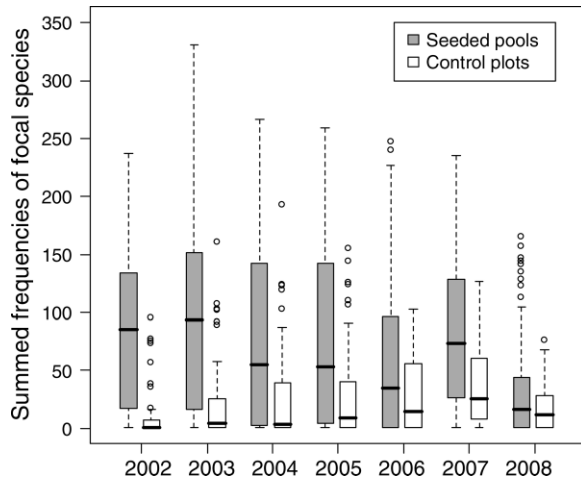


FIG. 1. Effects of seeding on the abundance of focal species in experimentally constructed vernal pools at Travis Air Force Base in Solano County, California, USA: summed frequencies of five focal species in seeded pools vs. control pools for the seven years (2002–2008) following the final seeding treatment in 2001. Dark horizontal lines represent medians, boxes contain upper (75%) and lower (25%) quartiles, and dashed whiskers contain the range of the data excepting outliers. Outliers (lying outside the box by more than 1.5 times the interquartile range) are represented by open circles. Frequency was measured using a square frame divided into 100 subquadrats over the marked plot in each pool and recording the number of subquadrats out of 100 in which the species occurred.

control pools for four of the five focal species (Table 2). The exception was *E. vaseyi*, which increased in frequency in both seeded and control pools (Table 2).

*Priority effects*

Of the four species subject to seeding priority treatments, only *Layia chrysanthemoides* failed to exhibit a strong priority effect (Fig. 2). For at least four

years (2002–2005) following the final seeding treatment, three species were found with much higher frequency in pools in which they were seeded first (e.g., group A species in group A priority pools) than in pools in which they were seeded one year after other species had been seeded (e.g., group B species in group A priority pools). Both *D. danthonioides* and *E. vaseyi* were seeded first in group A priority pools and both species occurred with higher frequency in group A priority pools, at least through 2005 (high and positive priority effect; Fig. 2). *Eryngium vaseyi* retained its priority effect through 2008. Both *Layia chrysanthemoides* and *P. stipitatus* were seeded first in group B priority pools, but only *P. stipitatus* occurred with much higher frequency in group B priority pools. The priority effect exhibited by *P. stipitatus* was lost after 2005. By 2006, priority effects were not evident for any species except *E. vaseyi*. Even for *E. vaseyi*, the priority effect declined steadily over time (Fig. 2).

Priority effects may decline through a loss in species frequency (e.g., a loss of group A species in group A priority pools) or through a gain (e.g., an increase in group B species in group A priority pools). Here, we observed that for group A species, frequencies tended to converge under both treatments as a result of both loss from pools in which they were seeded first (group A priority pools) and gain in pools in which they were seeded second (group B priority pools). For group B species, frequencies converged under both treatments mainly as a result of loss from group B priority pools (Fig. 3).

*Effects of seeding frequency*

One species, *L. conjugens*, was seeded either once (in 1999) or in three consecutive years (1999–2001). Any obvious effects of seeding frequency on the abundance

TABLE 2. Differences between seeded and control pools in the annual frequencies of each of the five focal species listed in Table 1.

Species and treatment	2002		2003		2004		2005		2006		2007		2008	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
LACO														
Seeded	31.61	4.89	33.40	5.14	24.48	4.79	23.94	4.85	5.84	2.47	25.17	7.38	4.05	1.91
Control	0.00	0.00	0.42	0.24	0.37	0.19	0.03	0.03	0.03	0.02	1.18	0.63	0.38	0.28
ERVA														
Seeded	23.31	2.56	27.87	2.61	30.72	2.69	28.35	2.56	44.47	3.42	42.52	3.73	26.28	2.20
Control	2.69	0.68	5.72	1.04	7.91	1.29	7.50	1.22	21.45	2.59	18.28	2.34	12.88	1.57
DEDA														
Seeded	22.44	2.74	21.67	2.97	26.98	3.26	21.37	3.00	9.76	1.98	27.20	4.35	2.30	1.04
Control	0.48	0.22	2.58	1.05	6.82	1.97	5.18	1.54	2.05	0.81	10.68	2.95	0.88	0.45
LACH														
Seeded	9.08	1.55	8.78	1.61	3.71	0.74	4.27	1.01	1.50	0.72	0.44	0.24	0.83	0.35
Control	0.01	0.01	0.00	0.00	0.03	0.03	0.16	0.12	0.35	0.35	0.41	0.36	0.12	0.12
PLST														
Seeded	26.19	3.29	34.76	3.59	12.38	2.36	24.72	3.03	10.40	1.96	3.52	1.47	1.07	0.45
Control	5.12	1.67	8.06	2.23	5.75	1.80	9.22	2.27	0.88	0.33	2.12	1.08	0.56	0.27

Notes: For seeded pools, each mean is calculated using data from every pool that received seeds of the given species, regardless of the variation in seeding treatments described in Table 1. Frequency was measured using a square frame divided into 100 subquadrats placed over the marked plot in each pool and recording the number of subquadrats out of 100 in which the species occurred. Species abbreviations are: LACO, *Lasthenia conjugens*; ERVA, *Eryngium vaseyi*; DEDA, *Deschampsia danthonioides*; LACH, *Layia chrysanthemoides*; PLST, *Plagiobothrys stipitatus*.

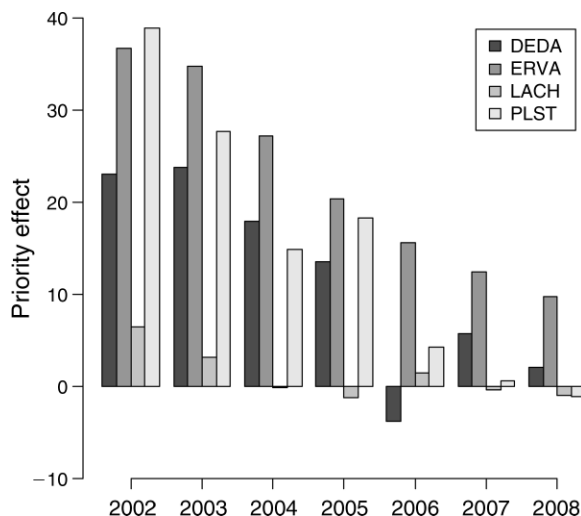


FIG. 2. Priority effects resulting from two different treatments applied to the seeded pools shown in Fig. 1. Darker bars represent group A species (DEDA and ERVA); lighter bars, group B species (LACH and PLST) (Table 1). Half of the treatment pools received seeds of group A species in 1999, followed by seeds of group B species in 2000; the other half received seeds of group B species in 1999, followed by group A species in 2000. If there were priority effects, we would expect a species to occur more frequently where it was seeded first. In this figure, each "priority effect" is the mean frequency of the species in pools in which it was seeded in 1999 minus its mean frequency in pools in which it was seeded in 2000. For all species, evidence of a priority effect declines with time. For most species, there is little evidence for priority effects after 2006, a year of extreme weather. Species abbreviations are: DEDA, *Deschampsia danthonioides*; ERVA, *Eryngium vaseyi*; LACH, *Layia chrysanthemoides*; PLST, *Plagiobothrys stipitatus*.

of *Lasthenia conjugens* persisted for only four years after the final seeding treatment in 2001. During this period, the relative dominance of *L. conjugens* in more frequently seeded pools caused shifts in community composition between these two treatments. By 2006, this species had reached generally low abundance in both seeded and control pools (Table 2 and Fig. 4).

#### Precipitation anomaly, 2006

In 2006, we observed a substantial decline in the abundance and frequency of nearly all vernal pool species, including four of the five focal species, in experimental pools (Figs. 1, 4, and 5). The 2005–2006 winter wet season was unusual and clearly affected plant growth and development. Specifically, rainfall in January and February 2006 was average, but rainfall in March and April was over three times greater than the average for those months: 35.13 cm in 2006 vs. a 50-year average of 11.43 cm. The precipitation anomaly observed in March and April of 2006 has occurred only twice in the past 50 years. We observed high mortality of vernal pool plants during our field sampling in late April 2006 and surmised that these plants had emerged but succumbed to the unusually high late-spring water

levels. Overall abundance of four of the five planted species in experimental pools declined 55–81% compared to their abundances in 2005 (*D. danthonioides*, –55%; *Lasthenia conjugens*, –81%; *Layia chrysanthemoides*, –60%; *P. stipitatus*, –67%). However, *E. vaseyi*, the sole perennial species of the group, nearly doubled in average abundance, showing an 84% increase in 2006 compared to 2005. Thus, observations in 2006 revealed abrupt changes in the trajectories of individual species and communities in experimental pools.

#### Abiotic context and magnitude of priority effects

The priority effects that we observed in group A and group B priority pools (Fig. 2) were not uniform among pools of different water depths. For group A priority pools, the magnitude of the priority effect increased with increasing water depth and peaked in pools between 10 and 15 cm in depth (Fig. 6). The AIC<sub>c</sub> values for the saturating and null models were, respectively, 5.39 and 18.55 units higher than for the quadratic model, suggesting that the quadratic model was much better

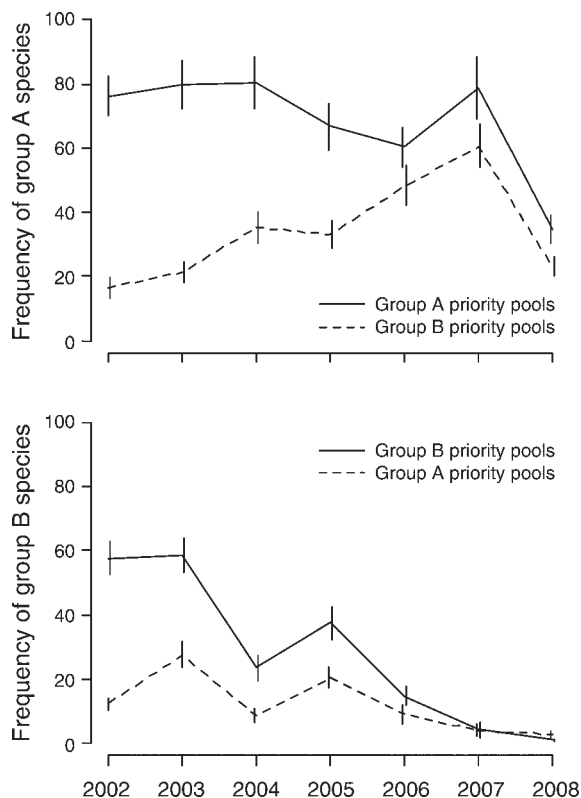


FIG. 3. Temporal patterns of convergence in the frequency of species between pools in which they were seeded in the first year (solid lines) vs. the second year (dashed lines). The frequency of group A species (upper panel) declined where they were seeded first but increased where they were seeded second. The frequency of group B species (lower panel) declined regardless of seeding priority. *Lasthenia conjugens* was excluded from this analysis, because it occurred in both groups. See Fig. 1 for an explanation of frequency measurements and Fig. 2 for an explanation of group composition.

supported by the data. For group B priority pools, we detected no association between the strength of the priority effect and pool depth (Fig. 6).

#### DISCUSSION

Observations from the first seven years of plant community formation in this field experiment provide compelling evidence for (1) dispersal limitation of vernal pool species, (2) priority effects in plant species composition, (3) shifts in the relative abundance of species as a result of increased frequency of colonization, and (4) context dependence in biological interactions among species. Each of these findings suggests a key role for historical contingency in the early stages of community development. But we also observed that each of these effects was transient. In this system, historical effects appear to have been lost within a decade. In other words, while assembly rules may have had important effects on the early trajectories of these communities, these communities are now tending toward a similar endpoint. Here we discuss the various patterns contributing to temporal variation in community structure.

Dispersal limitation was evident in our study despite the proximity of natural vernal pools within 15–150 m of our experimental pools and despite the even shorter distance (10 m) between neighboring experimental pools. Dispersal limitation has been demonstrated in other field studies of plant community restoration (e.g., Foster et al. 2007, Trowbridge 2007). For example, Foster et al. (2007) added seeds of 32 native tallgrass prairie species to study plots in an abandoned hayfield in northeastern Kansas, USA, and left other plots unseeded. They observed strong effects of seeding on plant species diversity and species composition. In a study of floodplain restoration in the Central Valley of California, Trowbridge (2007) found evidence for dispersal limitation in one, but not the other, of the two floodplains studied. Although seeding may not be necessary if ample seed sources exist nearby and there are no physical barriers to dispersal (e.g., Robinson et al. 2002), our study demonstrates that even very short distances between vernal pools can present surprisingly effective barriers to seed dispersal, even after several years of potential seed bank development.

It is likely that dispersal limitation, in conjunction with declining frequencies of focal species in seeded pools, led to poor cover of most focal species in later years. By 2008, unseeded, control pools had been colonized by only a small number of individuals of the five focal species. The more limited the rate of dispersal, the longer it should take for a species to become as common in control pools as in treatment pools. For two of the focal species (*D. danthonioides* and *E. vaseyi*), frequencies in control pools tended to rise throughout the seven years of this experiment, suggesting a dispersal-limited process. It is more difficult to infer dispersal limitation for the remaining species, because

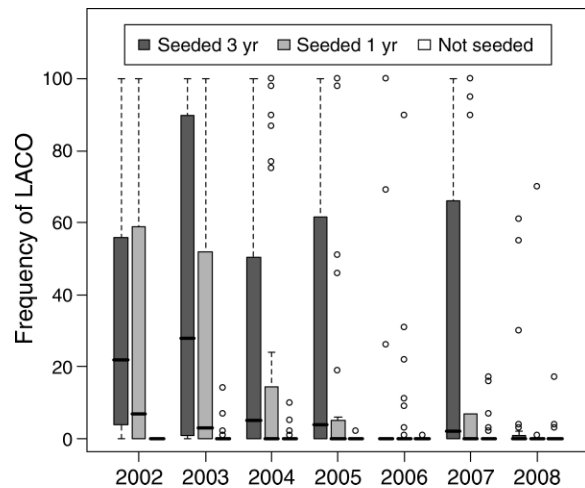


FIG. 4. Effects of seeding frequency on the frequency of *Lasthenia conjugens* (LACO) in experimentally created vernal pools. Seeding treatments were applied in the first year or in the first three years after pool creation (see Table 1). LACO was typically absent from unseeded control pools, as indicated by boxes with zero height. See Fig. 1 for an explanation of frequency measurements and a description of the box plots.

their frequencies clearly declined in treatment pools and either declined (*P. stipitatus*) or remained very low (*Lasthenia conjugens* and *Layia chrysanthemoides*) in control pools. Although dispersal limitation may have contributed to these patterns, we can only infer that conditions were generally unfavorable for these three species during our experiment.

If dispersal limitation is a factor in population establishment, then both the frequency and timing of colonization events or seeding treatments must be considered during community development. Frequency and timing are interdependent, because events that occur more frequently are more likely to be timed, at least once, during a period when the event could have an impact. For example, our experiment demonstrated that *Lasthenia conjugens* was at first more abundant in pools seeded in 1999, 2000, and 2001 compared to those seeded only in 1999. This effect may have depended mainly on seeding frequency and consequent differences among treatments in seed bank development. Alternatively, this effect may have depended mainly on timing: i.e., the single-year seeding treatment would be inferior if 1999 was a poor year for seed survival. We interpret our results in terms of seeding frequency in part because there is no evidence for a strong effect of timing given the observed weather in 1999 and in part because frequency generally trumps timing. In any case, effects of seeding frequency disappeared in a year when the timing of precipitation was extremely unusual (2006) and remained weakened throughout the low-precipitation years of 2007 and 2008. It remains to be seen whether the difference between seeding treatments will have long-lasting effects on the seed bank that may

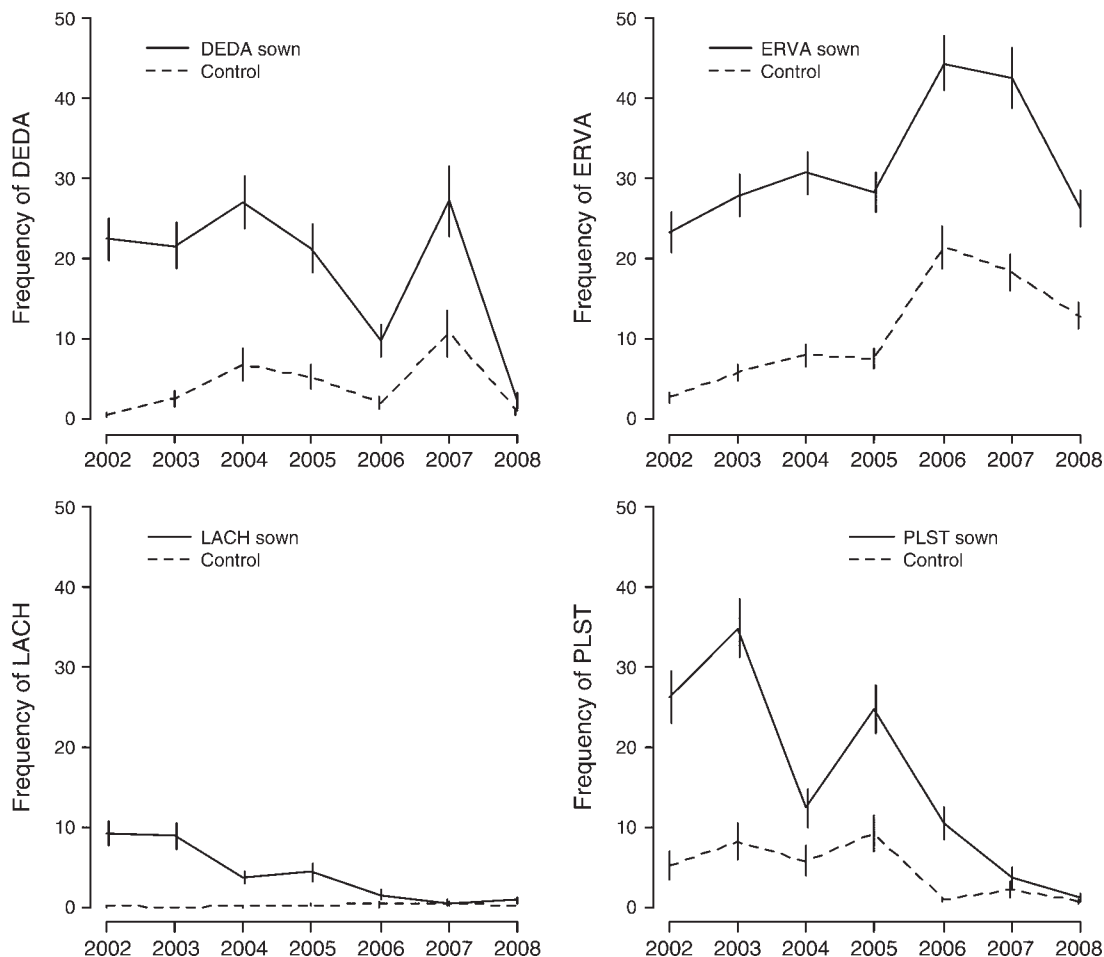


FIG. 5. Mean frequencies of each of the four "priority treatment" species in seeded vs. control pools over the sampling period 2002–2008. The solid line in each graph is the mean frequency in pools in which the species was seeded, and the dashed line is the mean frequency in pools in which it was not seeded (including control pools and pools seeded only with *Lasthenia conjugens*; see Table 1). See Fig. 1 for an explanation of frequency measurements and Fig. 2 for an explanation of species abbreviations.

allow *L. conjugens* to rebound more strongly in pools in which it was seeded more frequently.

Although the combined frequency of focal species generally increased in both seeded and control pools in early years, it generally decreased in seeded pools after 2005. We suggest three possible reasons for these declines. First, all species except *E. vaseyi* declined sharply in 2006 due to the anomalously high precipitation noted previously. During the following winter, 2006–2007, the study site received much lower total winter precipitation than average (33.08 cm vs. 55.16 cm). These two consecutive "bad-weather" events may have depleted the seed bank of these annual species. As the sole perennial member of this group, *E. vaseyi* may have been able to maintain its abundance through these harsh conditions because of its underground resources. Indeed, *E. vaseyi* has shown no severe declines, despite population fluctuations, in the seven years following seeding. A second, related possibility is that *E. vaseyi* may outcompete annual species due to its perennial

habit and relatively large, branching growth form. When four of the five focal species declined in 2006, this may have given *E. vaseyi* a competitive advantage that persisted through 2008. Third, the past two low-precipitation years (there was also lower-than-average precipitation in 2007–2008) have been accompanied by an increase in the abundance of invasive exotic species, to the point at which litter from these exotics may be compromising emergence of the native vernal pool annuals (S. K. Collinge, unpublished data). Previous studies of this system (Gerhardt and Collinge 2007) have shown that high precipitation early in the growing season can reduce survival of several key exotic species in these pools; but the past two years have had relatively low early-season precipitation, suggesting prime conditions for enhanced performance of exotic species.

Priority effects have been observed in several recent experiments with grassland communities. For example, Fukami et al. (2005) created experimental plots with various seed mixtures on former agricultural land and

showed that initial differences in plant species composition caused communities to diverge in species identity over a nine-year period. But their study also revealed convergence in the predominance of species with similar traits over the same time period. In particular, despite different initial conditions, all plots eventually became dominated by one of the species trait groups, which consisted of tall, patch-forming perennials. In our study, we seeded only one perennial species (*Eryngium vaseyi*), so we cannot address the issue of trait group dominance. Notably, *E. vaseyi* is relatively abundant but is not necessarily dominant in naturally occurring vernal pools at our study site, so these plant communities do not necessarily converge to a stable equilibrium dominated by *E. vaseyi*. In a more controlled study of grassland species in a glasshouse and common garden setting, Körner et al. (2008) sowed seeds of species belonging to different plant functional groups (e.g., herbs, grasses, and legumes) and observed that small differences in arrival time (three weeks) resulted in priority effects that persisted for the two field seasons during which they conducted their study. Our results suggest that even strong priority effects observed in the first few seasons may soon be lost, lending less predictability to long-term community trajectories.

In the early phase of community formation, we observed strong priority effects for three of the four species in the priority seeding treatments. For *D. danthonioides* and *E. vaseyi*, both seeded in group A, these effects were quite strong, whereas for the group B species, these effects were weaker (*P. stipitatus*) or nonexistent (*Layia chrysanthemoides*). The strength of each priority effect was correlated with the relative abundance of each species in reference pools at this study site: *D. danthonioides* and *E. vaseyi* occur with higher relative abundance than *P. stipitatus* and *L. chrysanthemoides*, suggesting that perhaps they are stronger competitors within these experimental pools.

The trajectories of community development that we observed in our priority group treatments reversed during our seven-year period of observation. For the first four years after seeding, group A and group B priority plots diverged distinctly in species composition. Thereafter, pools from different treatments converged in species composition toward similar endpoints. If we had stopped collecting data in 2005, we would have concluded that these results were consistent with the model of “alternative stable states” in community ecology (e.g., Suding et al. 2004, Young et al. 2005). Our observations from 2006 to 2008, however, are consistent with the notion of a single, stable equilibrium for vernal pool plant communities. However, we know from observations of naturally occurring pools at this site that species composition is not identical for all pools. The fact that the strong, early priority effects disappeared later in the study underscores the need for long-term studies of community dynamics. This is not to say that short-term observations are meaningless for

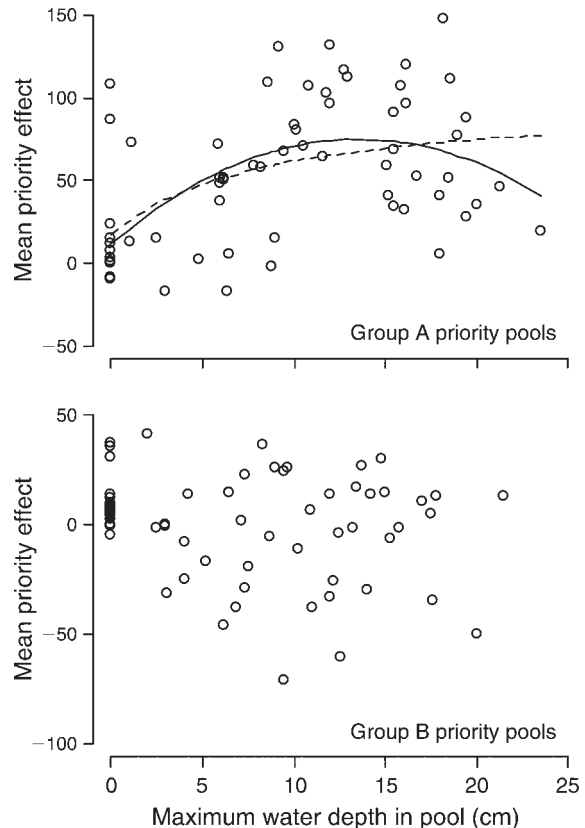


FIG. 6. Interactions between water depth and priority effects in vernal pool plant communities. “Priority effect” is defined here as the difference between the cover (summed frequencies) of species found only in the first group seeded into the pool and the cover of species found only in the second group seeded into the pool (Table 1). Priority effects were averaged across years (2002–2008) and plotted against the maximum water depth measured in each pool. Water depth may be related to mean priority effect by a saturating model (dashed line) or by a quadratic model (solid line). For group A priority pools (upper panel), the data are best described by a quadratic model ( $\Delta AIC_c = 5.31$  for the saturating model, 11.62 for the null model), suggesting that priority effects were most prevalent in pools of intermediate depth. For group B priority pools (lower panel), there was no evidence of lasting priority effects at any water depth.

long-term, community dynamics, especially when seed banks are considered. Little is currently known about the persistence of seeds in vernal pool plant communities, but this is an active area of research. Our limited observations suggest that seeds can remain dormant but viable for decades at this site (S. K. Collinge, unpublished data). In the spring of 2000, we identified flowering individuals of several native vernal pool plant species in newly created basins that were previously unrecorded from this site. Because the experimental pools were created on land that was plowed for crop production in the first half of the 20th century, it is unlikely that these plant species had experienced appropriate seed germination conditions for several decades. The early priority

effects that we observed in our experiment allowed the buildup of seed banks of priority group species in respective treatments, so there is the possibility that priority effects could reassert themselves in the future.

In addition to our observations of transience (or perhaps temporal variability) in priority effects, we also found that the strength of the priority effect varied with environmental context, depending on the water depth of the pools. For group A pools, where *D. danthonioides* and *E. vaseyi* were the dominant species, the strength of the priority effect was highest in pools of intermediate depth. This suggests that the strength of interspecific interactions that are responsible for this effect varied in relation to water depth as well. For group B pools, where *P. stipitatus* and *L. chrysanthemoides* were dominant in the early years, priority effects were relatively weak even in those early years. It is perhaps because priority effects were weak in group B pools that there was no detectable shift in the priority effect with depth. There are few empirical studies of shifts in the magnitude of priority effects along environmental gradients (Agrawal et al. 2007). From our observations, we conclude that the effect of the abiotic (water depth) gradient was only apparent in one of the two biotic contexts (priority group treatments).

In summary, we observed significant but transient effects of seeding, order of colonization, and frequency of colonization on species abundances and community composition. We will continue to examine trajectories of community assembly in this system, to determine whether these transient effects will reemerge, perhaps as a result of seed bank development. Alternative outcomes include further convergence of assembly trajectories toward a single, perhaps stable endpoint or some form of system "reboot" in which the extreme weather of 2006 initiates a new community assembly process. Differentiating these outcomes should be possible by following these experimental communities whose histories are well characterized.

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