

## LETTER

## Rainfall variability maintains grass-forb species coexistence

Lauren M. Hallett,<sup>1\*</sup>  
 Lauren G. Shoemaker,<sup>2</sup>  
 Caitlin T. White<sup>3</sup> and  
 Katharine N. Suding<sup>3</sup>

<sup>1</sup>Environmental Studies Program  
 and Department of Biology University of Oregon Eugene, OR 97403,  
 USA

<sup>2</sup>Botany Department University of Wyoming Laramie, WY 82071, USA

<sup>3</sup>Institute of Arctic and Alpine Research University of Colorado Boulder Boulder, CO 80309, USA

\*Correspondence: E-mail:  
 hallett@uoregon.edu

### Abstract

Environmental variability can structure species coexistence by enhancing niche partitioning. Modern coexistence theory highlights two fluctuation-dependent temporal coexistence mechanisms — the storage effect and relative nonlinearity — but empirical tests are rare. Here, we experimentally test if environmental fluctuations enhance coexistence in a California annual grassland. We manipulate rainfall timing and relative densities of the grass *Avena barbata* and forb *Erodium botrys*, parameterise a demographic model, and partition coexistence mechanisms. Rainfall variability was integral to grass–forb coexistence. Variability enhanced growth rates of both species, and early-season drought was essential for *Erodium* persistence. While theoretical developments have focused on the storage effect, it was not critical for coexistence. In comparison, relative nonlinearity strongly stabilised coexistence, where *Erodium* experienced disproportionately high growth under early-season drought due to competitive release from *Avena*. Our results underscore the importance of environmental variability and suggest that relative nonlinearity is a critical if underappreciated coexistence mechanism.

### Keywords

*Avena*, California grasslands, *Erodium*, fluctuation-dependent, modern coexistence theory, rangelands, relative nonlinearity, resource acquisitive, storage effect, stress tolerant.

Ecology Letters (2019) 22: 1658–1667

### INTRODUCTION

Understanding the processes that allow a diversity of species to coexist is a longstanding and fundamental question in the field of community ecology. Throughout the history of community ecology, the concept of the niche has been integral to different formalisations of how species can coexist (Grinnell 1917; Hutchinson 1957; Holt 2009; Levine & HilleRisLambers 2009). Niche dynamics operate when species are more limited by themselves than others, allowing populations to increase when rare and stabilising the coexistence of multiple species (Chase & Leibold 2003). While niches can stabilise coexistence in consistent environments, environmental variability can further promote niche-based coexistence by increasing the potential for niche partitioning between species (May & MacArthur 1972; Chesson 2000b). For example, tradeoffs between resource acquisitive and stress tolerant strategies may enhance species coexistence in environments with high resource variability (Angert *et al.* 2009; Hallett *et al.* 2017). Environmental fluctuations not only alter species' ability to partition niche space, but can also modulate the strength of competition experienced in different environments, shifting community compositions and altering species coexistence (Germain *et al.* 2018). Given that environmental fluctuations are ubiquitous in natural systems, the role of environmental variability in structuring diversity has emerged as a core component of coexistence theory (Chesson 1994, 2018).

Modern coexistence theory has gained traction as a powerful tool to understand how species differences and the abiotic environment jointly structure species diversity (Chesson 2000b, 2008). Critically, coexistence theory highlights the importance of environmental variability for coexistence and provides a framework to partition fluctuation-dependent

processes that promote coexistence between species (formalised temporally in Chesson 2000b and spatially in Chesson 2000a). Within coexistence theory, the storage effect and relative nonlinearity have emerged as dominant fluctuation-dependent mechanisms of coexistence in temporally variable environments (Chesson 2018). The temporal storage effect quantifies the ability of species to capitalise on good years while 'storing' individuals through poor years, with seed banks as a classic example (Warner & Chesson 1985; C'aceres 1997). For a storage effect to promote coexistence, three criteria must occur: (1) species-specific responses to environmental variability, (2) covariance between environment and competition, and (3) buffered (i.e. sub-additive) population growth (Chesson 2000b; Ellner *et al.* 2016). While the storage effect depends on species-specific responses to the environment, relative nonlinearity can maintain coexistence if species have a nonlinear response to variability in competitively limiting environmental conditions. Relative nonlinearity enhances coexistence potential when species experience relatively stronger increases in growth in favourable conditions compared to more minimal decreases in growth in unfavourable environmental conditions (Chesson 2000b).

While modern coexistence theory has consistently highlighted the importance of environmental variability for species coexistence, there have been relatively few empirical tests (but see Angert *et al.* 2009; Descamps-Julien & Gonzalez 2005; Adler *et al.* 2010; Letten *et al.* 2018). This is due in large part to two roadblocks, the first mathematical and the second practical. First, the most commonly-adopted model to partition the role of stabilising vs. equalising forces was solved under average conditions (Godoy *et al.* 2014). Consequently, most empirical tests of coexistence, even those in variable environments, have focused on species performance and the relative role of

stabilising vs. equalising mechanisms under average conditions (Levine & HilleRisLambers 2009; Godoy *et al.* 2014; Kraft *et al.* 2015). These are valuable tests that highlight the conditions that promote coexistence, but they cannot partition the importance of environmental variability. Second, data requirements to assess fluctuation-dependent coexistence are non-trivial, because of the dependence on multiple, varying environmental conditions and species observations at a range of abundances and competitive conditions (e.g. Sears & Chesson 2007; Bimler *et al.* 2018). As a result, there have been few attempts to experimentally test the storage effect and relative nonlinearity. Instead, the majority of empirical studies that investigated fluctuation-dependent coexistence have depended on using long time series of demographic data to parameterise specific analytical models solved for coexistence mechanisms (Angert *et al.* 2009; Adler 2014; Chu & Adler 2015).

Recent quantitative developments may provide a path forward to testing the role of fluctuation-dependent coexistence in natural systems. To overcome the computational intensity of empirical tests, simulation-based inference has been proposed to test the storage effect (Ellner *et al.* 2016). More recently, Ellner *et al.* (2019) have proposed a computational approach that partitions the storage effect as well as other coexistence mechanisms such as relative nonlinearity in an empirically-tractable way, creating a bridge between theoretical developments in coexistence theory and general empirical applications. Combining this approach with experimental data may be a particularly powerful way to isolate when and how environmental fluctuations promote coexistence. For example, a difference in species' regeneration niches has been a long-standing example of how variability may promote coexistence (Grubb 1977). Many plant species have environmentally driven germination cues, which can generate episodic recruitment events that bolster the population over time (Bartolome 1979; Larson *et al.* 2015; Larson & Funk 2016). Experimentally manipulating environmental conditions during recruitment windows may allow us to parse the dynamics that underlie patterns in observational studies. Such an approach dovetails with a growing body of literature suggesting that coexistence mechanisms in general are often shaped by early differences in recruitment niches (Chu & Adler 2015; Usinowicz *et al.* 2017).

Here, we take an experimental approach to partition when and how fluctuation-dependent mechanisms operate and understand their role in promoting coexistence. We focus on California grasslands, which are dominated by annual, Mediterranean grasses and forbs and experience a high level of rainfall variability. Species composition is highly variable in this system, and has classically been described as shifts between 'grass years' and 'forb years' (Talbot *et al.* 1939; Pitt & Heady 1978; Dudley *et al.* 2017). These shifts have been associated with the amount and timing of rainfall, with high early-season rainfall favouring resource-acquisitive grasses and early-season drought favouring more stress-tolerant forbs (Pitt & Heady 1978; Hallett *et al.* 2017). This pattern of grass and forb years, combined with the annual life cycle and well-studied seed bank dynamics of the composite species (Rice 1985), make California grasslands an excellent system to test the role of fluctuation-dependent mechanisms on species coexistence. We experimentally created four different intra-annual rainfall

patterns in the field, under which we manipulated the ratios and densities of the dominant grass, *Avena barbata*, and dominant forb, *Erodium botrys* (nomenclature follows Baldwin *et al.* 2012). We used these data to simulate population change under constant vs. variable inter-annual rainfall conditions, testing the hypothesis that temporal variation in early-season rainfall maintains species coexistence. Second, we applied recent computational advances (Ellner *et al.* 2019) to partition the contribution of mechanisms reflective of the storage effect and relative nonlinearity for coexistence.

## MATERIALS AND METHODS

### Study site

We conducted the experiment in a valley grassland at the Sierra Foothill Research Extension Center near Brown's Valley, CA, USA (39°15' 04.2" N 121° 18' 39.0" W, Elev. 202 m). The site has a Mediterranean climate with cool, wet winters and hot, dry summers. The growing season is typically initiated by germinating rains in October and runs through April. Most rainfall occurs during this period, but the amount and timing of rainfall varies substantially between years [growing season rainfall averages 717 mm but has ranged from 220 to 1263 mm over the past 50 years (PRISM Climate Group, 2004)]. Rainfall during the experimental growing season (2014–2015) totaled 545 mm. The site was situated on a gentle south-facing slope with reddish loam soil. Vegetation at the site is characteristic of California grasslands: dominant grasses include *Avena barbata*, *Festuca perenne*, and *Bromus hordeaceus*; common forbs include *Erodium botrys* and *Trifolium hirtum* (nomenclature follows Baldwin *et al.* 2012).

### Experimental design

In fall 2014, we established four rainfall treatments in a random block design, with plots arranged in a single row from east to west. Blocks were replicated four times for a total of 16 plots. Early-season rainfall in this system is thought to primarily affect recruitment, whereas late-season rainfall primarily affects growth. To isolate the effect of drought on periods of recruitment vs. growth, our rainfall treatments consisted of early-season fall dry, late-season spring dry, consistent dry and a consistent wet control. Dry treatments were achieved using 6.4 × 5.2 m cold frame rainout shelters with clear polyethylene retractable roofs. We erected the roofs shortly before rainfall events, and removed them afterward to minimise their effect on solar radiation. Following the first germinating rains, we experimentally created our rainfall treatments by applying the roofs in some seasons and not others, with a goal of reducing precipitation by 50% during target seasons. To create early-season fall dry we applied roofs during storms from Oct to Jan, for late-season spring dry from Feb to Apr, and for consistent dry from Oct to Apr. We monitored soil moisture using five soil moisture probes in each plot (EC-5, Decagon Devices Inc, Pullman WA USA), inserted vertically to measure average volumetric water content of 5–10 cm depth. Sensors were calibrated and corrected for variability due to factors such as incomplete contact between sensor and soil by

normalising measurements to gravimetric measurements of maximum field capacity ( $0.50\text{ m}^3/\text{m}^3$ ) and minimum air-dried moisture content in late summer ( $0.04\text{ m}^3/\text{m}^3$ ). Rainfall manipulations effectively decreased soil moisture at 5–10 cm depth by up to 50% (Figure S1).

Within each main plot, we manipulated the seeding density and ratio of the dominant grass *Avena barbata* to the dominant forb *Erodium botrys* (hereafter *Avena* and *Erodium*) to assess the recruitment and growth dynamics of each species when it was rare vs. common. Prior to treatment implementation, we reduced the extant seed bank by removing the existing vegetation and upper  $\approx 3$  cm of top soil. We seeded at two total densities on a log-scale: low ( $320\text{ seeds}/\text{m}^2$ ) and high (similar to observed stem densities,  $3200\text{ seeds}/\text{m}^2$ ). At each density we manipulated the seeding ratio of *Avena* to *Erodium* to capture a range from rare to common (0:10, 1:9, 5:5, 9:1, and 10:0 *Avena:Erodium*). This yielded a total of  $10\ 25 \times 25$  cm subplots per main rainfall plot for a total of 160 subplots. We collected the seeds for both species on-site the year prior to the experiment to minimise any effects of local adaptation. The two species had roughly comparable seed weights (*Avena*:  $0.0013 \pm 0.00040$  g/seed) and *Erodium*:  $0.0015 \pm 0.00044$  g/seed), which minimised potential effects of a seed mass vs. seed number tradeoff.

We measured initial recruitment by counting stems by species in December, and we measured fecundity by counting species' seed production in the spring. To account for differences in phenology, we measured *Erodium* fecundity in late March and *Avena* in late April. Both species retain evidence of seed production following seed release (*Erodium* retains its sepals and *Avena* its spikelets). Consequently, we measured fecundity toward the end of seed production and multiplied each indicator by accordant seeds produced (5 seeds are produced per *Erodium* flower head and 2 per *Avena* spikelet).

## Analysis

### Recruitment and population growth rate

To assess the effect of rainfall, seeding ratio, and density on each species' dynamics we used linear mixed effect models with rainfall treatment (categorical), seeding ratio (continuous) and density (categorical) as fixed effects, rainfall by seeding ratio and density by seeding ratio as interaction terms, and block as a random effect. We modelled each species separately and used two response variables to capture differences in recruitment vs. fecundity: (1) recruitment, calculated as the number of stems in December as a proportion of the number of seeds added, and (2) per capita population growth rate, calculated as the number of seeds produced divided by the number of seeds added.

To project species' population growth rates under different environmental conditions, we employed a two-species discrete-time competition model that reflects the dynamics in our annual system (Levine & HilleRisLambers 2009). The population growth rate of focal species  $x$  in competition with species  $y$  is:

$$\frac{N_{x,t+1}}{N_{x,t}} = s_x(1 - g_x) + \frac{\lambda_{x,t}g_x}{1 + \alpha_{xx,t}g_xN_{x,t} + \alpha_{xy,t}g_yN_{y,t}} \quad (1)$$

here,  $N_{x,t}$  is the number of viable seeds of species  $x$  at the beginning of the growing season at time  $t$ . The first term of the sum describes the carryover of seeds in the seed bank, where  $s_x$  is the annual survival of seeds in the seed bank and  $g_x$  is the fraction of seeds that germinate. The second term describes population growth and annual seed production. Here,  $\lambda_{x,t}$  is the number of viable seeds produced in the absence of intra- and inter-specific competition at time  $t$ ,  $\alpha_{xx,t}$  describes the per-capita intraspecific competitive effect on the number of seeds produced, and  $\alpha_{xy,t}$  is the per-capita inter-specific competitive effect at time  $t$ . We used the Beverton-Holt competition function because it has been well-suited to similar systems (Levine & HilleRisLambers 2009; Larios *et al.* 2017). We fit the model for each of the four rainfall treatments, allowing  $\lambda_{x,t}$ ,  $\alpha_{xx,t}$ , and  $\alpha_{xy,t}$  to vary across time based on the current rainfall condition. We used maximum likelihood on a log-transformed eqn using the *nlsLM* function from package *minpack.lm* (Elzhov *et al.* 2015) in R version 3.4.2 (R Core Team 2013). Initially we allowed for facilitation ( $\alpha$  values  $< 0$ ). However, because facilitation was only observed in a single case and was slight ( $\alpha_{xy,t} = -0.005 \pm 0.003$  for *Avena* competing with *Erodium* in consistent wet conditions), and the population model does not allow for coexistence, we constrained both  $\alpha$  and  $\lambda$  values to  $> 0$ .

Seed bank dynamics of *Erodium* and *Avena* have been extensively studied elsewhere, and we used literature-derived terms for seed survival and germination estimates. Both species have persistent seed banks, but *Erodium* has both higher seed bank carryover and longer seed viability. Specifically, *Erodium* has *c.* 60% of seeds germinate across drought and 64% of seeds germination across wet conditions (Rice 1985). Following a year in the seed bank, the remaining seeds maintain a viability of 82% (Rice 1985), and seeds remain viable over multiple years (at least 30 years) (Hull 1973). In contrast, *Avena* has higher rates of initial germination (estimated 90% across conditions), and lower seed survival in the seed bank (40%) (Young *et al.* 1981; Larios *et al.* 2017).

### Calculating coexistence

To test for stable coexistence, we used the mutual invasion criterion with the invader-resident comparison (Chesson 2000b; Barabás *et al.* 2018). Stable coexistence occurs if each species can invade when the resident community (here the resident species, since we are comparing a two-species case) is at its steady state abundance distribution (i.e. its equilibrium distribution given the underlying time-heterogeneity in rainfall conditions). A species' growth rate as the invader compared to the resident (average growth rate when rare; GRWR) determines how quickly a species can recover from low-density. Growth rate at a given time  $t$  is defined as  $r_x = \ln \frac{N_{x,t+1}}{N_{x,t}}$ . The average GRWR across environmental conditions is given by  $\bar{r}_i$ , and we compare the invader ( $i$ ) to resident ( $r$ ) such that we calculate average GRWR as  $\bar{r}_i - \bar{r}_r$ . Because the resident is at steady state and there is a negligible effect of the invader,  $\bar{r}_r$  is approximately equal to 0, such that  $\bar{r}_i = \bar{r}_i - \bar{r}_r$ . Comparing the invader and resident is important, however, as coexistence can be fostered by factors that either help the invader or hinder the resident, and therefore this comparison has important implications for mechanistic partitioning of coexistence



(Ellner *et al.* 2019). Stable coexistence in a two-species model occurs if all species have a positive average GRWR. Conversely, a species with a negative average GRWR is predicted to be driven towards competitive exclusion, and stable coexistence of the community does not occur.

Using simulations, we tested conditions under which both *Avena* and *Erodium* exhibited positive GRWR and therefore stable coexistence. We first determined each species' GRWR for each of our four rainfall treatments. To do so, we first set *Erodium* as the resident species, and used eqn 1 to determine its equilibrium abundance for each rainfall condition without *Avena* present. We then invaded a single seed of *Avena* into the resident *Erodium* community and calculated its GRWR. We subsequently followed the same methodology, but with *Avena* as the resident and *Erodium* as the invader.

To test if stable coexistence occurred under variable environmental conditions, we assessed coexistence in relation to historic rainfall patterns. We characterised historical rainfall patterns using monthly mean precipitation data from 1896 to 2016 for Brown's Valley (PRISM Climate Group, O. S. U. 2004). We considered the year to be 'early-season dry' if fall but not spring rainfall was below average, 'late-season dry' if spring but not fall rainfall was below average, 'consistent dry' if both seasons were below average, and 'consistent wet' if both seasons were above average. Under these criteria, across the time series 50% of years were consistent dry, 12% of years were early-season dry, 12% of years were late-season dry, and 26% of years were consistent wet. We used these rainfall patterns to simulate the resident's steady state abundance distribution. We defined the first 49 years as a 'burn-in' period to remove any effect of initial starting conditions (this was conservative, as the model tended to equilibrate after *c.* 5 time steps), and calculated GRWR for the invader over the subsequent 72 years. We then calculated the invader's average GRWR across variable conditions,  $\bar{r}_i - \bar{r}_r$ , by averaging across the 72 years. Finally, we modelled expected *Avena* and *Erodium* abundance across the entire timeseries (1896 to 2016), incorporating environmental effects on  $\lambda_{x,t}$ ,  $\alpha_{xx,t}$ , and  $\alpha_{xy,t}$ . For this simulation, we set initial abundances of each species to their average abundance after the 'burn-in' simulation.

#### Partitioning coexistence mechanisms

Finally, we decomposed GRWR for each species into the mechanisms that contribute to coexistence of *Avena* and *Erodium* in variable environments. Following the decomposition of Ellner *et al.* (2019), we decompose  $\bar{r}_i - \bar{r}_r$ , examining the effect of fluctuations in seed production ( $\lambda$ ) and fluctuations in the competitive environment ( $\alpha$ ):

$$\bar{r}_i = \bar{r}_i - \bar{r}_r = \Delta_i^0 + \Delta_i^\alpha + \Delta_i^\lambda + \Delta_i^{\alpha\lambda}. \quad (2)$$

here, the first decomposition term, ( $\Delta_i^0$ ), is the difference in average population growth rates between the invader and resident under constant environmental conditions. We set the constant environmental condition to be the weighted mean condition from 1945 to 2016. The second decomposition term,  $\Delta_i^\alpha$  is *relative nonlinearity in alpha* and is analogous to the *relative nonlinearity in competition* term from Chesson 2000. Chesson's relative nonlinearity in competition quantifies the

contribution of fluctuations in the intensity of competition, and here  $\Delta_i^\alpha$  quantifies the closely related effect of environmental variation on competition coefficients. Specifically, it is calculated as each species' growth rates when rare with variable  $\alpha$  minus growth rates with no variability. Similarly,  $\Delta_i^\lambda$  is *relative nonlinearity in seed production* and quantifies the main effect of environmentally-driven variation in intrinsic seed production. Finally,  $\Delta_i^{\alpha\lambda}$  quantifies the interaction effect not accounted for by the main effects in isolation. It is composed of two parts, a term analogous to the *classic storage effect* and a variance–interaction term introduced by Ellner *et al.* (2019). This variance–interaction term is absent in classic modern coexistence theory due to the requirement of small variance approximations for analytical tractability (Chesson 2000b; Barabás *et al.* 2018), but can also contribute to coexistence when the assumption of small variances is relaxed (Ellner *et al.* 2019). The Ellner *et al.* (2019) approach provides a pathway to more closely tie theory with experiments, and to relate coexistence mechanisms explicitly with the biology of the system. For example, the approach allows us to focus on the relative nonlinearity of seed production compared to the relative nonlinearity of competition, providing insight into the biology underlying coexistence. The mechanisms are analogous although not equivalent to the mechanisms partitioned by Chesson (2000b). The full derivation of the decomposition closely follows the *Cyclotella pseudostelligera* and *Fragilaria crotonensis* example from Ellner *et al.* (2019) and is provided in our Supplementary Methods. An extension of the decomposition to directly align with Chesson (2000b) is available in the Supplementary Methods of Ellner *et al.* (2019).

#### Sensitivity analysis

To test the significance of our coexistence partitioning, we first used a leave-one-out analysis in which we ran our model and calculated coexistence mechanisms for every combination of three from the four replicates as well as the full dataset. Second, because we could not extend this approach to literature-derived seed germination and seed survival terms, we conducted a sensitivity analysis to examine how changes in these parameters altered coexistence mechanisms. We randomly sampled each term from a uniform distribution ranging from  $\pm 25\%$  of its observed value, fit the population models and calculated coexistence mechanisms. We repeated this process 10 000 times.

## RESULTS

### Recruitment and population growth rate

*Avena* recruitment rates decreased with a higher proportion of conspecifics (seeding ratio) and with total density but were unaffected by rainfall (Figure S2, Table S1). Similar to recruitment, *Avena* growth rates decreased with seeding ratio and density, and the effect of seeding ratio was lessened with increasing density (Fig. 1; see Table S2 for effect sizes and *P*-values). Unlike recruitment, however, *Avena* growth rates were greatly elevated under consistent wet conditions, and there was an interaction in which the effect of seeding ratio was strengthened under this condition (Fig. 1, Table S2).

Similar to *Avena*, *Erodium* recruitment rates also decreased with seeding ratio and density, and the effect of seeding ratio was lessened with density (Figure S2, Table S3). Unlike *Avena*, however, *Erodium* recruitment was affected by rainfall. *Erodium* recruitment rates were suppressed under early-season wet conditions (both the consistent wet and late-season dry treatment), and the effect of seeding ratio was lessened under consistent wet conditions (Figure S2, Table S3). *Erodium* population growth responses were similar to recruitment dynamics. Growth rates decreased with seeding ratio and density, and the negative effect of seeding ratio was lessened with higher density (Fig. 1, see Table S4 for effect sizes and *P*-values). Rainfall treatment effects diverged slightly, in that growth rates were lowest under consistent wet conditions and were marginally significantly higher under fall early-season dry conditions (Fig. 1, Table S4). Both species had high viability in the system, with nearly all individuals successfully recruiting at low densities under favourable environmental conditions (Figure S2).

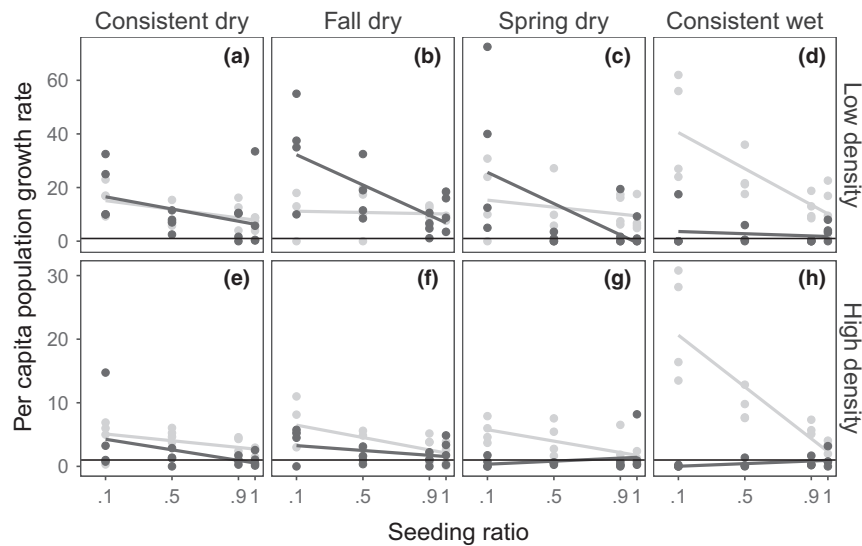
Using the above dynamics, we fit our two-species discrete-time competition model (Table 1) for *Avena* and *Erodium* under each environmental condition. *Avena* had a high intrinsic growth rate, producing between 7.3 and 21.3 seeds per individual in the absence of competition. Despite significant effects of seeding ratio and density, both intra- and inter-

specific competition terms were small for *Avena*. In contrast, *Erodium* dynamics depended more substantially on rainfall condition, with  $\lambda$  ranging from 1.1 to 157; both intra- and inter-specific competition were stronger for *Erodium*.

#### Coexistence in variable environments

Using our competition model, we examined coexistence dynamics for each species across environmental conditions. *Avena* could persist across all four rainfall conditions; that is, it had a positive GRWR under all treatments when invading *Erodium* under steady state conditions (Fig. 2, Figure S3). *Avena* growth rate was highest under the consistent wet rainfall treatment, and correspondingly lowest under the consistent dry treatment. In contrast, *Erodium* could only increase when rare under treatments that experienced drought during the recruitment period (i.e., early-season fall dry and consistent dry conditions; Fig. 2, Figure S3). Under treatments with wet early-season conditions (consistent wet and late-season spring dry), *Erodium* exhibited a negative GRWR, suggesting that *Erodium* would be competitively excluded by *Avena* in an environment with consistently high early-season rainfall.

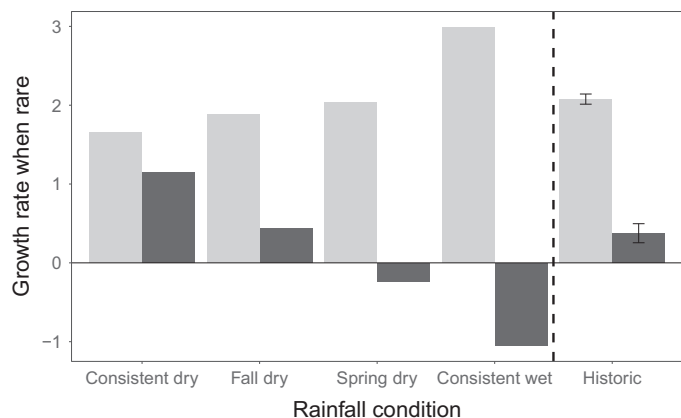
When incorporating observed environmental variability from the past 72 years of the historic record, we found that both *Avena* and *Erodium* were able to coexist, as both had a positive average GRWR. Under variable rainfall conditions



**Figure 1** Per-capita seed production as a function of seeding ratio, rainfall treatment (consistent dry, early-season fall dry, late-season spring dry, consistent wet control) and density treatment. Light grey indicates *Avena* and dark grey indicates *Erodium*. Populations can increase when the growth rate is  $> 1$  (black line).

**Table 1** Parameter estimates ( $\pm$ SE) for each focal species under varying rainfall conditions

Rainfall treatment	<i>Avena</i>			<i>Erodium</i>		
	$\lambda$	$\alpha_{ii}$	$\alpha_{ij}$	$\lambda$	$\alpha_{ii}$	$\alpha_{ij}$
Consistent dry	12.18 $\pm$ 2.99	0.02 $\pm$ 0.01	0.01 $\pm$ 0.01	23.25 $\pm$ 31.30	0.28 $\pm$ 0.45	0.01 $\pm$ 0.04
Early season fall dry	7.33 $\pm$ 3.44	0.02 $\pm$ 0.01	0 $\pm$ 0.01	156.99 $\pm$ 835.17	1 $\pm$ 5.54	0.22 $\pm$ 1.30
Late season spring dry	8.61 $\pm$ 5.53	0.03 $\pm$ 0.04	0 $\pm$ 0.01	3.21 $\pm$ 3.39	0.06 $\pm$ 0.10	0.02 $\pm$ 0.04
Consistent wet	21.27 $\pm$ 5.30	0.02 $\pm$ 0.01	0 $\pm$ 0.01	1.06 $\pm$ 0.73	0.01 $\pm$ 0.02	0.03 $\pm$ 0.04

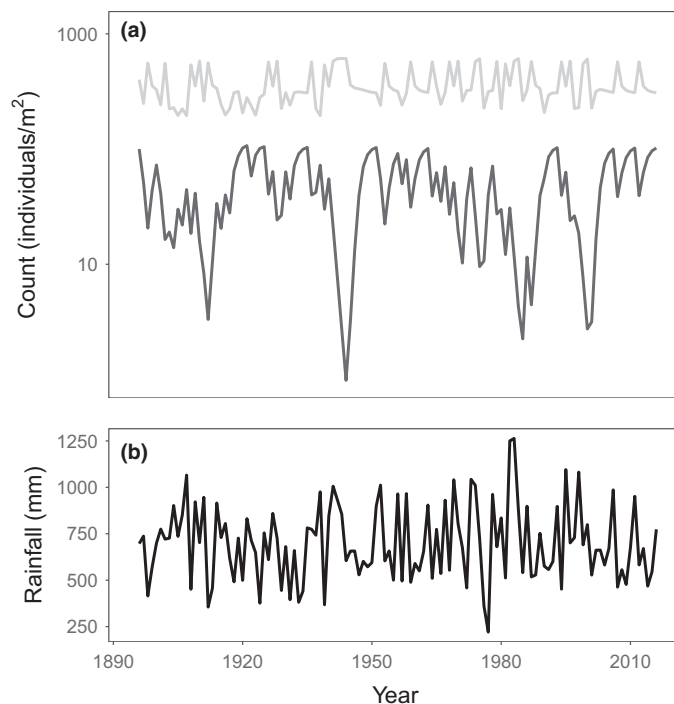


**Figure 2** Mutual invasion criterion for coexistence for *Avena* (light grey) and *Erodium* (dark grey) for each rainfall condition (consistent dry, early-season fall dry, late-season spring dry, consistent wet control) and historically experienced conditions from 1945 to 2016. Growth rates are calculated when the focal species is rare and the other is at its equilibrium population abundance; populations can increase when the logged growth rate is  $> 0$ .

both species could, on average, invade when the other species was at its steady state distribution. This yielded stable coexistence due to fluctuating environmental conditions (Fig. 2). Rainfall conditions altered both seed production and competition for *Erodium*, while primarily altering seed production for *Avena* (except in consistent dry conditions, where interspecific competition increased; Table 1). These different effects resulted in highly variable modelled population dynamics over the past 120 years, mirroring the highly variable community composition patterns observed in rangeland literature (Pitt & Heady 1978; Fig. 3).

Partitioning the mechanisms that allow for coexistence shows that, overall, environmental variability promotes coexistence for both *Avena* and *Erodium* by increasing their GRWR ( $\bar{r}_i$ ) (Fig. 4). While both species exhibited positive growth rates when rare under average historical conditions, variation in rainfall increased GRWR (comparing  $\bar{r}_i - \bar{r}_r$  to  $\Delta_i^0$ ). This increase in GRWR from variable environmental conditions in turn increased the probability of long-term coexistence, even with natural fluctuations in realised growth rates due to stochasticity (Schreiber *et al.* 2018).

Coexistence was promoted by different fluctuation-dependent mechanisms for *Avena* than *Erodium*. *Avena* had strong potential for coexistence in the absence of environmental variability, and coexistence was furthered via the interaction effect of fluctuating environmental conditions on both alpha and intrinsic seed production ( $\Delta_i^{\alpha\lambda}$ ) (Fig. 4). This interaction term encapsulates both the effect of variance *per se* in  $\alpha$  and  $\lambda$  and the storage effect (Chesson 2000b; Barabás *et al.* 2018). In contrast, *Erodium* coexistence was promoted by environmentally-driven variation in alpha (i.e. *relative nonlinearity in alpha*,  $\Delta_i^{\alpha}$ ) (Fig. 4). Due to nonlinear responses, gains in GRWR for *Erodium* during beneficial years outweighed losses during poor conditions; this effect was driven both by changes in *Avena*'s steady-state abundance as the resident and reduced interspecific competition for *Erodium* when it was the invading species. Relative nonlinearity in both competitive effects ( $\alpha$ ) and seed production ( $\lambda$ )

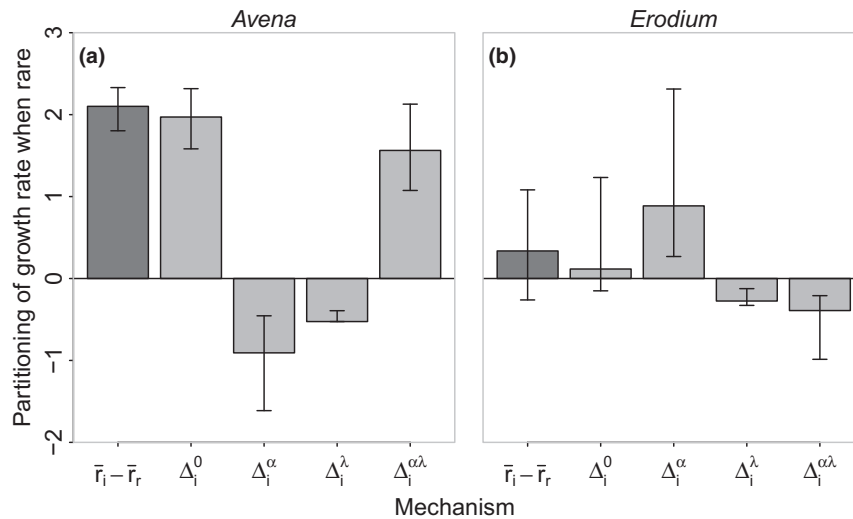


**Figure 3** (a) Simulated population dynamics for *Avena* (light grey) and *Erodium* (dark grey) based on (b) historic rainfall records from 1896 to 2016. Here, we considered the year to be 'early-season dry' if fall but not spring rainfall was below average, 'late-season' dry if spring but not fall rainfall was below average, 'consistent dry' if both seasons were below average, and 'consistent wet' if both seasons were above average.

was slightly destabilising for *Avena* whereas relative nonlinearity in seed production ( $\lambda$ ) and the storage effect were slightly destabilising for *Erodium* (Fig. 4). Variation in estimated seed germination and seed survival parameters had minimal effect on coexistence mechanisms (Figure S4).

## DISCUSSION

Modern coexistence theory has highlighted the importance of environmental variability for species coexistence. Nonetheless, empirical tests of the strength and mechanism of fluctuation-dependent coexistence have lagged behind theory. Here, we integrate recent developments in coexistence theory (Ellner *et al.* 2019) with a natural history pattern of 'grass vs. forb years' in California grasslands (Pitt & Heady 1978). We experimentally demonstrate that rainfall variability – and in particular, the periodic occurrence of early-season drought – is essential for grass-forb coexistence in an annual grassland. While the storage effect has captured greater theoretical and empirical attention than relative nonlinearity, in our system both mechanisms were in operation, their effects differed by species and relative nonlinearity was the more critical mechanism for stable coexistence. In particular, the relative benefit of early-season drought on the growth rate of the dominant-forb *Erodium* was far higher than the relative cost under wet conditions, a benefit due to release in competition from the dominant-grass *Avena*. Our results provide strong empirical evidence that environmental variability is integral to



**Figure 4** Partitioning the role of environmental variability on growth rate when rare ( $\bar{r}_i - \bar{r}_r$ ) for (a) *Avena* and (b) *Erodium*. Overall low density growth rate is decomposed into the growth rate with no environmental variability ( $\Delta_i^0$ ), the main effect of the environment affecting competition coefficients ( $\Delta_i^\alpha$ ), the main effect of the environment affecting growth rate ( $\Delta_i^\lambda$ ), and the interactions term with environment affecting both competition and growth rates ( $\Delta_i^{\alpha\lambda}$ ). Error bars show the entire range of values from the leave one out analysis.

coexistence, and that relative nonlinearity in competitive effects (alpha) is a critical if underappreciated coexistence mechanism.

Rainfall variability enhanced the growth rates of both *Avena* and *Erodium*, but only *Erodium* required variability to persist in the system. Specifically, *Avena* was favoured in wet years but could increase when rare across all rainfall conditions, whereas *Erodium* could only increase in years with early-season drought. Fluctuation-dependent coexistence mechanisms are often assumed to be reciprocal (i.e., both species require fluctuations to persist) or treated as such in theoretical literature for mathematical ease (Chesson 2000b; Shoemaker & Melbourne 2016), but our findings suggest that fluctuation-dependent mechanisms can have an asymmetrical effect on differing species. Some species (e.g. *Avena*) may not require fluctuations to persist, while community coexistence may still depend on fluctuations creating a positive GRWR for other species (e.g. *Erodium*). Our findings are similar to those of Adler *et al.* (2006), who demonstrated that some perennial plants need environmental variation, whereas others can maintain populations across environmental conditions. This pattern may be ubiquitous across systems, as some species specialise on specific environmental conditions while others act more as generalists with large niche breadths. Further empirical tests of coexistence, especially considering more diverse communities, will help elucidate the generality of this pattern.

Multiple fluctuation-dependent mechanisms may structure patterns of coexistence. Here we found that the strength and directional effect of different mechanisms varied by species. Specifically, the storage effect was stabilising for *Avena* but not *Erodium*, whereas relative nonlinearity in alpha was stabilising for *Erodium* but not *Avena*. Given average fitness differences between the species, relative nonlinearity in alpha was integral for *Erodium* to maintain grass-forb coexistence. Our results underscore the importance of partitioning multiple mechanisms of coexistence and indicate that relative nonlinearity may be a critical stabilising mechanism in natural systems. Our

results parallel recent work focused on nectar yeasts communities, within which relative nonlinearity is a key coexistence mechanism, but the strength of different coexistence mechanisms differs by species (Letten *et al.* 2018). While the storage effect is the most commonly imputed fluctuation-dependent mechanism of coexistence, we find that it can also play a destabilising role. This result mirrors theoretical work by Holt & Chesson (2014), who found that strong asymmetry in species germination resulted in a negative storage effect for some species, destabilising coexistence. Paralleling our results, in this case coexistence only occurred from other mechanisms, such as average fitness differences, which overcame the destabilising role of the storage effect and the variance-interaction term.

Species-specific environmental responses are a fundamental component of fluctuation-dependent coexistence models. At the same time, competition is a strong force in this and other systems, especially during periods of recruitment (in California grasslands, it is common for around 50% of seedlings to be thinned from the community during this time (Bartolome 1979; Young *et al.* 1981). Recent work by Germain *et al.* (2018) has highlighted that competition can mediate differential species responses and persistence across variable environments. Specifically, they found that patterns of coexistence (and a lack thereof) that might be imputed to species-specific environmental responses in observational studies are in fact governed by environment-species interactions in which the strength of competition varies with the environment. Along the same lines, we found that, despite minimal interspecific competitive effects (i.e., small  $\alpha$  values), competition was a driving force in structuring coexistence dynamics. In particular, fluctuation in interspecific competition promoted coexistence for *Erodium* via relative nonlinearity. As such, the biological reason underlying *Erodium* coexistence is a competitive release under some environmental conditions (as opposed to intrinsically favouring those conditions). Relatedly, simulations in this system suggest that environmental variability has



the potential to enhance forb persistence by mediating competition, even when forbs prefer the same conditions as grasses. Specifically, successive unfavourable years reduce grass seed availability and therefore their competitive pressure, allowing forbs to increase in a subsequent favourable year (Levine & Rees 2004). While a Chesson (2000b) partitioning should similarly indicate the importance of relative nonlinearity, the Ellner *et al.* (2019) partitioning allows further insight into the biology of this coexistence mechanism. Our results accentuate the important role of environment-species interactions in modern coexistence theory, and further underscore the value of experiments to partition the mechanisms governing coexistence.

Our findings additionally highlight the importance of regeneration niches for species coexistence. We found that *Erodium* exhibited a differential response to rainfall in its recruitment phase, and that this difference persisted to affect end-of-season fecundity. These results add to the growing recognition that strong niche differences can emerge at the recruitment phase. For example, Adler *et al.* (2010) and Chu & Adler (2015) partitioned niche differences for periods of recruitment, growth, and survival among perennial plants and found disproportionately large niche differences during recruitment. Similarly, trait differences that emerge during the first few weeks of growth can scale to affect species composition and diversity (Larson *et al.* 2015; Larson & Funk 2016). A marked regeneration niche may be due to a combination of processes: species-specific germination cues (Daws *et al.* 2002), environmentally-dependent patterns of germinant mortality (Bartolome 1979; Young *et al.* 1981), and high exposure to interspecific competition (Garcia-Serrano *et al.* 2007). In our system these processes may have combined to contribute to *Erodium*'s pronounced regeneration niche. In particular, stress-tolerant traits may increase the probability that *Erodium* germinants survive early-season drought while also benefiting from reduced competition from *Avena*. We expect early-season rainfall will generate consistent tradeoffs between resource-acquisitive grasses and stress-tolerant forbs common to the system, whereas other variables may enhance partitioning within functional groups. For example, Rice & Menke (1985) found that later spring rainfall had a differential effect on different species of *Erodium*.

A pattern of grass vs. forb years has long been dogma for California grasslands, but whether or not this pattern is driven by rainfall has been a subject of debate (Duncan & Woodmansee 1975). Our findings suggest that rainfall does indeed drive tradeoffs in the growth rates of the dominant grass and forb, but how these tradeoffs affect annual composition is likely due to rainfall patterns over multiple years. For example, recent analyses suggest that lag effects from rainfall in the previous year affect annual grassland composition as much as concurrent rainfall, with grasses favoured by previously wet years and forbs by previously dry (Dudney *et al.* 2017). Our findings suggest that seed input is a likely mechanism for this lag, given that both species could produce many seeds regardless of initial population size under their favourable conditions. As such, rainfall over successive years should combine to affect observed species composition, with previous years affecting seed availability and the current year affecting recruitment (especially for forbs). We observed this effect in

our simulation over historic rainfall conditions, with periodically large declines and gains in *Erodium* abundance associated with multi-year rainfall patterns.

While our focus has been on historic rainfall patterns, climate variability is expected to increase in California, with the potential for both more extreme intra-annual rainfall patterns as well as multi-year extreme events (Swain *et al.* 2018). Our simulation results suggest that extended extreme weather patterns may increase variability in *Erodium* abundance, with several successive wet years generating large declines in *Erodium* populations. At the same time, rainfall is only one component of the variability that structures California grasslands. Spatial variability in litter levels and soil compaction may promote niche partitioning, with *Erodium* able to colonise bare areas and self-drill into compacted areas (Stamp 1984; Rice 1985). Similarly, the majority of California grasslands are cattle grazed. Increased grazing intensity is also associated with a higher proportion of *Erodium* (Stein *et al.* 2016; Hallett *et al.* 2017), providing another mechanism for forb coexistence. Applying our understanding of fluctuation-dependent coexistence to predicted climate variability and integrating spatial and temporal variation within empirical tests are key avenues to understanding coexistence now and in the future.

#### ACKNOWLEDGEMENTS

We thank Jared Huxley, Joan Dudney, Andrew Moyes, Whendee Silver, Dustin Flavell, Nikolas Schweitzer and the crew at the Sierra Foothills Research and Extension Center for help with project implementation. We thank Stephen Ellner for feedback on the analyses, and comments from editor Dr. Robin Snyder, reviewer Dr. Gyuri Barabás and two anonymous reviewers which greatly improved the manuscript. Research was supported by USDA grant \#2014 – 67019 – 21613 and a G. A. Harris Research Instrumentation Fellowship. LMH was supported by a USDA NIFA Pre-Doctoral Fellowship (\#2015 – 67011 – 22829) and a Philomathia Fellowship. LGS was supported by The James S. McDonnell Foundation grant \#220020513. Data and code are available at: <https://github.com/laurenmh/avena-erodium>.

#### DATA ACCESSIBILITY STATEMENT

All data are available on Figshare under the DOI: <https://doi.org/10.6084/m9.figshare.8298266.v1>. Model code is available on Github at <https://github.com/laurenmh/avena-erodium>.

#### AUTHORSHIP

LMH and KNS designed the experiment, LMH and CTW conducted the fieldwork, LMH and LGS created and analysed the population models, LGS partitioned coexistence mechanisms, LMH and LGS wrote the paper and KNS and CTW edited it.

#### REFERENCES

Adler, P. (2014). Testing the storage effect with long-term observational data. In: *Temporal Dynamics and Ecological Process* (eds Kelly, C.,



- Bowler, M. & Cox, G. (2002). Cambridge University Press, Cambridge, pp. 82–101.
- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl Acad. Sci.*, 103, 12793–12798.
- Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: an embarrassment of niches. *Ecol. Lett.*, 13, 1019–1029.
- Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci.*, 106, 11641–11645.
- Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J. & Wilken, D.H., eds. (2012). *The Jepson Manual: Vascular Plants of California*. Second edition, thoroughly revised and expanded edition edn. University of California Press, Berkeley, Calif. ISBN 978-0-520-25312-4.
- Barabás, G., D'Andrea, R. & Stump, S.M. (2018). Chesson's coexistence theory. *Ecol. Monogr.*, 88, 277–303.
- Bartolome, J.W. (1979). Germination and seedling establishment in california annual grassland. *J. Ecol.*, 273–281.
- Bimler, M.D., Stouffer, D.B., Lai, H.R. & Mayfield, M.M. (2018). Accurate predictions of coexistence in natural systems require the inclusion of facilitative interactions and environmental dependency. *J. Ecol.*, 106, 1839–1852.
- C'aceres, C.E. (1997). Temporal variation, dormancy, and coexistence: a field test of the storage effect. *Proc. Natl Acad. Sci.*, 94, 9171–9175.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press.
- Chesson, P. (1994). Multispecies competition in variable environments. *Theor. Pop. Biol.*, 45, 227–276.
- Chesson, P. (2000a). General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.*, 58, 211–237.
- Chesson, P. (2000b). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Chesson, P. (2008). Quantifying and testing species coexistence mechanisms. In: *Unity in Diversity: Reflections on Ecology After the Legacy of Ramon Margalef* (eds Valladares, F., Camacho, A., Elosegui, A., Gracia, C., Estrada, M., Senar, J.C. & Gili, J.M.). Fundacion BBVA, Bilbao, pp. 119–164.
- Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity. *J. Ecol.*, 106, 1773–1794.
- Chu, C. & Adler, P.B. (2015). Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecol. Monogr.*, 85, 373–392.
- Core Team, R. (2013). *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Daws, M., Burslem, D.F.R.P., Crabtree, L.M., Kirkman, P., Mullins, C. & Dalling, J.W. (2002). Differences in seed germination responses may promote coexistence of four sympatric piper species. *Funct. Ecol.*, 16, 258–267.
- Descamps-Julien, B. & Gonzalez, A. (2005). Stable coexistence in a fluctuating environment: an experimental demonstration. *Ecology*, 86, 2815–2824.
- Dudney, J., Hallett, L.M., Larios, L., Farrer, E.C., Spotswood, E.N., Stein, C. *et al.* (2017). Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands? *J. Ecol.*, 105, 484–495.
- Duncan, D.A. & Woodmansee, R.G. (1975). Forecasting forage yield from precipitation in california's annual rangeland. *J. Range Manag.*, 327–329.
- Ellner, S.P., Snyder, R.E. & Adler, P.B. (2016). How to quantify the temporal storage effect using simulations instead of math. *Ecol. Lett.*, 19, 1333–1342.
- Ellner, S.P., Snyder, R.E., Adler, P.B. & Hooker, G. (2019). An expanded modern coexistence theory for empirical applications. *Ecol. Lett.*
- Elzhov, T.V., Mullen, K.M., Spiess, A.-N. & Bolker, B. (2015). minpack.lm: R interface to the levenberg-marquardt nonlinear least-squares algorithm found in minpack, plus support for bounds (ver. 1.2-0) r package.
- Garcia-Serrano, H., Sans, F. & Escarré, J. (2007). Interspecific competition between alien and native congeneric species. *Acta Oecol.*, 31, 69–78.
- Germain, R., Mayfield, M.M. & Gilbert, B. (2018). The filtering metaphor revisited: competition and environment jointly structure invasibility and coexistence. *Biol. Lett.*, 14, 20180460.
- Godoy, O., Kraft, N.J. & Levine, J.M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.*, 17, 836–844.
- Grinnell, J. (1917). The niche-relationships of the california thrasher. *Auk*, 34, 427–433.
- Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.*, 52, 107–145.
- Hallett, L.M., Stein, C. & Suding, K.N. (2017). Functional diversity increases ecological stability in a grazed grassland. *Oecologia*, 183, 831–840.
- Holt, R.D. (2009). Bringing the hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl Acad. Sci.*, 106, 19659–19665.
- Holt, G. & Chesson, P. (2014). Variation in moisture duration as a driver of coexistence by the storage effect in desert annual plants. *Theor. Popul. Biol.*, 92, 36–50.
- Hull, A. Jr (1973). Germination of range plant seeds after long periods of uncontrolled storage. *J. Range Manag.*, 198–200.
- Hutchinson, G. (1957). Concluding remarks: cold spring symposia on quantitative. *Biol.*, 22, 27–415.
- Kraft, N.J., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci.*, 112, 797–802.
- Larios, L., Hallett, L.M. & Suding, K.N. (2017). Where and how to restore in a changing world: a demographic-based assessment of resilience. *J. Appl. Ecol.*, 54, 1040–1050.
- Larson, J.E. & Funk, J.L. (2016). Regeneration: an overlooked aspect of trait-based plant community assembly models. *J. Ecol.*, 104, 1284–1298.
- Larson, J.E., Sheley, R.L., Hardegree, S.P., Doescher, P.S. & James, J.J. (2015). Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. *J. Appl. Ecol.*, 52, 199–209.
- Letten, A.D., Dhimi, M.K., Ke, P.-J. & Fukami, T. (2018). Species coexistence through simultaneous fluctuation-dependent mechanisms. *Proc. Natl Acad. Sci.*, 115, 6745–6750.
- Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254.
- Levine, J. & Rees, M. (2004). Effects of temporal variability on rare plant persistence in annual systems. *Am. Nat.*, 164, 350–363.
- May, R.M. & MacArthur, R.H. (1972). Niche overlap as a function of environmental variability. *Proc. Natl Acad. Sci.*, 69, 1109–1113.
- Pitt, M. & Heady, H. (1978). Responses of annual vegetation to temperature and rainfall patterns in northern california. *Ecology*, 59, 336–350.
- PRISM Climate Group, O. S. U. (2004). Prism climate data. URL <http://prism.oregonstate.edu/>.
- Rice, K.J. (1985). Responses of erodium to varying microsites: the role of germination cueing. *Ecology*, 66, 1651–1657.
- Rice, K.J. & Menke, J.W. (1985). Competitive reversals and environment-dependent resource partitioning in *Erodium*. *Oecologia*, 67, 430–434.
- Schreiber, S., Levine, J.M., Godoy, O., Kraft, N. & Hart, S. (2018). Does deterministic coexistence theory matter in a finite world? insights from serpentine annual plants. *bioRxiv*, 290882.
- Sears, A.L. & Chesson, P. (2007). New methods for quantifying the spatial storage effect: an illustration with desert annuals. *Ecology*, 88, 2240–2247.
- Shoemaker, L.G. & Melbourne, B.A. (2016). Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology*, 97, 2436–2446.
- Stamp, N.E. (1984). Self-burial behaviour of *Erodium cicutarium* seeds. *J. Ecol.*, 72, 611.
- Stein, C., Harpole, W.S. & Suding, K.N. (2016). Transitions and invasion along a grazing gradient in experimental california grasslands. *Ecology*, 97, 2319–2330.

- Swain, D.L., Langenbrunner, B., Neelin, J.D. & Hall, A. (2018). Increasing precipitation volatility in twenty-first-century California. *Nat. Clim. Chang.*, 8, 427.
- Talbot, M., Biswell, H. & Hormay, A.L. (1939). Fluctuations in the annual vegetation of California. *Ecology*, 20, 394–402.
- Usinowicz, J., Chang-Yang, C.-H., Chen, Y.-Y., Clark, J.S., Fletcher, C., Garwood, N.C. *et al.* (2017). Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity. *Nature*, 550, 105.
- Warner, R.R. & Chesson, P.L. (1985). Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.*, 125, 769–787.
- Young, J.A., Evans, R.A., Raguse, C.A. & Larson, J.R. (1981). Germinable seeds and periodicity of germination in annual grasslands. *Hilgardia*, 49, 1–37.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Robin Snyder

Manuscript received 4 March 2019

First decision made 18 April 2019

Second decision made 5 June 2019

Manuscript accepted 19 June 2019