Received: 22 February 2024 | Accepted: 30 September 2024

DOI: 10.1111/1365-2745.14451

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Fitness differences override variation-dependent coexistence mechanisms in California grasslands

Andrew J. Muehleisen[1] | **Caitlin T. White**[2] | **Lauren S. Shoemaker**[3] | **Katharine N. Suding**[2] | **E. Ashley Shaw Adams**[1,4] | **Lauren M. Hallett**[1]

[1]Institute of Ecology & Evolution, University of Oregon, Eugene, Oregon, USA

[2]Department of Ecology & Evolutionary Biology, University of Colorado, Boulder, Colorado, USA

[3]Botany Department, University of Wyoming, Laramie, Wyoming, USA

[4]Department of Biology, Appalachian State University, Boone, North Carolina, USA

Correspondence
Andrew J. Muehleisen
Email: amuehlei@uoregon.edu

Funding information
National Institute of Food and Agriculture, Grant/Award Number: 2014-67019-21613; Office of Integrative Activities, Grant/Award Number: 2019528; Division of Environmental Biology, Grant/Award Number: 2047239

Handling Editor: Xiang Liu

Abstract

1. While most studies of species coexistence focus on the mechanisms that maintain coexistence, it is equally important to understand the mechanisms that structure failed coexistence. For example, California annual grasslands are heavily invaded ecosystems, where non-native annuals have largely dominated and replaced native communities. These systems are also highly variable, with a high degree of rainfall seasonality and interannual rainfall variability—a quality implicated in the coexistence of functionally distinct species. Yet, despite the apparent strength of this variation, coexistence between native and non-native annuals in this system has faltered.
2. To test how variation-dependent coexistence mechanisms modulate failed coexistence, we implemented a competition experiment between two previously common native forbs and three now-dominant non-native annual grasses spanning a conservative-acquisitive range of traits. We grew individuals from each species under varying densities of all other species as competitors, under either wetter or drier early season rainfall treatments. Using subsequent seed production, we parameterized competition models, assessed the potential for coexistence among species pairs and quantified the relative influence of variation-dependent coexistence mechanisms.
3. As expected, we found little potential for coexistence. Competition was dominated by the non-native grass *Avena fatua*, while native forbs were unable to invade non-native grasses. Mutual competitive exclusion was common across almost all species and often contingent on rainfall, suggesting rainfall-mediated priority effects. Among variation-dependent mechanisms, the temporal storage effect had a moderate stabilizing effect for four of five species when averaged across competitors, while relative nonlinearity in competition was largely destabilizing, except for the most conservative non-native grass, which benefited from a competitive release under dry conditions.
4. *Synthesis*: Our findings suggest that rainfall variability does little to mitigate the fitness differences that underlie widespread annual grass invasion in California,

but that it influences coexistence dynamics among the now-dominant non-native grasses.

KEYWORDS
Avena, California grasslands, competitive exclusion, modern coexistence theory, native, non-native, rainfall seasonality, stabilizing mechanisms

1 | INTRODUCTION

The assessment and partitioning of the mechanisms that either maintain or undermine diversity is a continuous project in community ecology. Modern Coexistence Theory (MCT) generalizes these mechanisms as a relative balance between fitness versus niche differences, the latter of which facilitates stable coexistence and thus diversity (Chesson, 2000). However, of equal importance—and concern today—are the conditions under which coexistence fails. This can occur most dramatically and most consequentially during biological invasions, where non-native species outcompete and potentially exclude native organisms (Hobbs, 2000). When invasions threaten native diversity, MCT suggests this is because the average fitness of the invader overwhelms any potential coexistence mechanisms (Chesson, 2000). While significant work has gone into describing and characterizing the traits that make successful invasive species (e.g. Van Kleunen et al., 2010), much less work has explicitly applied MCT to understand when species fail to coexist during biological invasions.

Heavily invaded systems, such as California grasslands (Borer et al., 2007), can provide insight into the reasons why coexistence can fail, helping reconcile coexistence theory and invasion ecology. Thought to be previously dominated by perennial grasses and annual forbs, these systems have been subject to continuous introductions of non-native annual grasses and forbs, originating with the westward expansion of European colonists (D'Antonio et al., 2007; Jackson, 1985). Disturbance related to drought and overgrazing are thought to have further aided the establishment of non-native annual species, cementing their status as successful invaders (D'Antonio & Vitousek, 1992; Heady et al., 1977). Today, the native species of California grasslands have been heavily displaced by non-native annual species, such as wild oat (*Avena* spp.), leaving little residual natural cover and habitat, while non-native species have become dominant components of these communities (Heady et al., 1977; Huenneke, 1989; Keeley, 1990).

Although this directional shift in community composition is widespread, high rainfall variability characteristic of California grasslands supports the reshuffling of community composition within and across years (Heady et al., 1991; Pitt & Heady, 1978). Rainfall variability, particularly in the early growing season (fall), has been implicated in trade-offs and coexistence between functionally distinct non-native plant groups in California; wetter or drier growing seasons characterize 'grass' years and 'forb' years respectively (Bartolome, 1979; Hallett et al., 2019; Pitt & Heady, 1978). More generally, strong temporal variation in the environment can be an effective driver of coexistence (variation-dependent stabilizing mechanisms, Chesson, 2000) and has been identified as a key determinant of community composition in many ecosystems (e.g. Adler et al., 2006; Angert et al., 2009; Hallett et al., 2019; Sears & Chesson, 2007; Wainwright et al., 2019; Warner & Chesson, 1985). Their environmental variability and annual dominance has helped make California grasslands a model system for experimental tests of species coexistence (Kraft et al., 2015; Levine & HilleRisLambers, 2009), but few of these studies explicitly incorporate intra-annual variability (Hallett et al., 2019; Levine & Rees, 2004). Furthermore, it is less clear to what extent growing-season rainfall variability mediates competition between native forbs and non-native annual grasses. While drier early season conditions can provide a release from competition with non-native annual grasses, native forbs may benefit less from this climate niche than non-native forbs (Hallett et al., 2019) due to their evolutionary history with more resource-conservative native perennial grasses. The role that rainfall variability plays in invasion resistance or success is therefore a highly relevant question for California grasslands that can be tested experimentally.

Temporal variation in rainfall can support coexistence if competitors have different temporal niches, even if competitive exclusion should occur under average conditions. There are two mechanisms by which this coexistence can arise: temporal storage effect and relative nonlinearity. Under the temporal storage effect, favourable environments can be less favourable for dominant, 'resident' species because they face greater competition during these periods, while rare species benefit from reduced competition in favourable conditions (Barabás et al., 2018; Chesson, 2000). Importantly, annual plants can buffer their populations from extirpation by 'storing' the benefit of favourable environments as seed banks. Indeed, the temporal storage effect has received considerable empirical interest (and support) in annual plant systems (Angert et al., 2009; Pake & Venable, 1995).

Relative nonlinearity can further enhance the stabilizing effect of rainfall variability. Under relative nonlinearity, different functional responses among species for the same limiting resources create conditions in which competitors benefit more from favourable conditions than they are limited by detrimental conditions, thereby benefiting from environmental variability (Chesson, 2000). Relative nonlinearity has traditionally been overshadowed by the storage effect, partly due to theory suggesting it should apply to more limited circumstances (Chesson, 1994; Yuan & Chesson, 2015). However, recent empirical work has suggested that relative nonlinearity may be an underappreciated stabilizing mechanism in temporally varying environments (Hallett et al., 2019; Letten et al., 2018; Yuan & Chesson, 2015). In this sense, the storage effect and relative nonlinearity are two key pathways by which early season rainfall variability could mediate competition between functionally distinct native and non-native species in California grasslands, though the extent and the relative influence of each remains an open question. Robust applications of coexistence theory often predict competitive exclusion even among co-occurring species (Godoy & Levine, 2014; Kraft et al., 2015; Wainwright et al., 2019), but the relative roles of variation-dependent vs. -independent mechanisms in exclusion remain to be quantified.

In this study, we implemented a competition experiment between two species of functionally distinct native California forbs and three functionally distinct species of non-native annual grasses subject to rainfall manipulation in the early growing season (fall) when seeds germinate and composition is most sensitive to rainfall (Bartolome, 1979; Hallett et al., 2019; Pitt & Heady, 1978). We grew individuals of each species in a background of each other competitor to parameterize dynamical models of competition and species abundances, allowing us to assess predictions of coexistence versus competitive exclusion and their underlying mechanisms. Each competition plot was either left uncovered in the early growing season or covered with a rainfall exclusion shelter during rain events in the early growing season to simulate environmental variability. We then partitioned species growth rates as invaders to quantify the relative contribution of environmental variability to competitive outcomes and coexistence. We first hypothesized that non-native annual grasses would have greater fitness under averaged conditions than native annual forbs, consistent with their invasive status. Second, we hypothesized that early growing season rainfall variability would moderate this effect, bolstering native forbs and maintaining coexistence among non-native grasses via variation-dependent coexistence mechanisms.

2 | METHODS

2.1 | Study site

The field experiment was implemented at the Sierra Foothills Research and Extension Center (SFREC), in Brown's Valley, CA (39°15′04.2″ N 121°18′39.0″ W, 202 m elevation; field work permission was given by the SFREC research committee). The grassland is on a gentle south facing slope and the soils are reddish loam. The site experiences a Mediterranean climate with cool, wet winters and hot, dry summers. Rainfall is highly variable at this site: average annual rainfall is 717 mm but has ranged from 220 to 1263 mm in the past 50 years (PRISM Climate Group, 2004). Species germinate following the fall rains (typically between Sep-Nov) and senesce by May or June. The vegetation is predominantly annual and dominated by non-native annual grasses and forbs, while some native forbs are intermittently present at low abundances.

2.2 | Field experiment

In fall 2016 we established two rainfall treatments in a random-block design. Two replicates of each treatment were nested in four blocks for a total of 16 plots, 8 plots per treatment. Recruitment is strongly governed by early season rainfall, and these dynamics are thought to be the primary drivers of annual species composition (Bartolome, 1979; Hallett et al., 2019). Consequently, we focused on manipulating early season rainfall and compared an early growing-season drought treatment with an early season wet treatment, with ambient conditions for the remainder of the growing season. The early drought treatment was achieved using 6.4 × 5.2 m cold frame rainout shelters with clear polyethylene retractable roofs (see Appendix S3 for photos) and the early wet treatments were left uncovered. We waited until after the first germinating rains to implement the drought treatment. It was a higher rainfall year, with the site receiving 309 mm of rainfall from Oct-Dec 2016 (67th percentile historically), when the treatments were in effect and a total of 972 mm over the full growing season (Oct–Apr, rainfall from CIMIS Station ID 84; California Irrigation Management Information System (CIMIS), n.d.). We tracked soil volumetric water content with soil moisture probes (EC-5, Decagon Devices Inc., Pullman WA USA) at 5–10 cm depth and achieved approximately a 50% reduction in moisture in the early dry treatment (equating to a growing season in the 23rd percentile historically; see Appendix S8 for soil moisture in each treatment).

Within each main plot, we seeded a competition experiment in which five focal species were grown in monoculture across two different densities (low, high) in randomized 0.5 m × 0.5 m subplots. In each monoculture subplot we seeded target 'phytometers' of each of the other five species, giving all pairwise species combinations of low-density phytometers with monoculture resident species (see Appendix S4 for seeding densities). An additional control plot was included with phytometers of all five species without a competitive background, which helps disentangle density-independent growth rates from intraspecific competitive rate when fitting population models.

Species were chosen to represent past-dominant native forbs versus currently dominate non-native grasses in this system and to represent a spread in hypothesized responses to rainfall. We chose three non-native annual grasses that were characteristic of invasions in these systems and common at the site. We expected that non-native annual grasses would be generally favoured by wetter early season conditions, but within the functional group their rainfall responses would ordinate based on their traits: *Avena fatua* (more acquisitive traits, expected to be most favoured by rainfall), *Bromus hordeaceus* (somewhat acquisitive traits) and *Vulpia myuros* (more conservative traits, expected to be least favoured by rainfall; Figure S10; Butterfield & Suding, 2013). We chose two native annual forbs, *Eschscholzia californica* and *Lasthenia californica*, that historically were likely dominant species and that were still present at the site albeit in low abundances (note that the current composition of the system is almost entirely non-native).

We speculated that they once had occupied a similar niche to the non-native annual grasses, especially *L. california* as it is known to have high germination under wet conditions (Gulmon, 1992), but may now persist due to a release in competition under dry conditions. A sixth species, the non-native nitrogen fixing forb *Trifolium hirtum*, was also included in the experiment but exhibited erratic growth and fecundity, precluding the possibility of properly parameterizing populations model for this species. Parameter estimates derived from *T. hirtum* were consequently excluded from analyses, leaving five species for downstream analyses. All phytometers as well as a subsample of individuals from each monoculture were harvested at peak biomass (late April for forbs, late May for grasses), dried for 72 h at 120F degrees and weighed. We then used weight to allometrically estimate seed production (see Appendix S6 for details of the allometric relationships). We counted stem densities in the monocultures and when more than one phytometer established, allowing us to estimate total seeds produced relative to the number of seeds added.

2.3 | Models and parameterization

We used our experimental data to parameterize annual plant population models to project growth rates in different rainfall environments. We used the two-species discrete-time competition model for annual plants (Levine & HilleRisLambers, 2009), generalized to an arbitrary number of species:

$$\frac{N_{x,t+1}}{N_{x,t}} = s_x\left(1 - g_x\right) + \frac{\lambda_{x,t} g_x}{1 + \alpha_{xx,t} g_x N_{x,t} + \sum_{y=1}^{n} \alpha_{xy,t} g_y N_{y,t}}. \qquad (1)$$

Here, the population growth rate of species *x* (its population size as seeds in the next growing season, $N_{x,t+1}$, over its population size in the current growing season, $N_{x,t}$) is a function of its annual seed survival rate s_x, germination fraction g_x, and its production of new seeds. The first term $s_x(1-g_x)$ represents seed carry-over from the previous growing season. In the next term, λ_x is the intrinsic growth rate of focal species *x* (i.e. its expected viable seed production in the absence of either intra- or inter-specific competition). In the denominator, α_{xx} is the per-capita intraspecific competition coefficient (i.e. the effect of one conspecific on seed production), α_{xy} is the per-capita interspecific competition coefficient (i.e. the effect of one individual of species *y* on focal species *x*), and *n* is the number of interspecific competing species. If α_{xx} and α_{xy} are positive, then competition has a net negative effect on the reproduction of species *x*. Competition coefficients can be negative as well, suggesting a facilitative effect. Finally, λ and α are dependent on *t*, meaning both can vary with the growing conditions of that season.

Seed germination rates were derived from the literature where possible (see Appendix S5 for specific references). Because seed annual survival rates were difficult to derive from the literature for *Lasthenia californica* and *Vulpia myuros*, we assumed a uniformly low survival rate of 1%, which was similar to literature-derived estimates. Due to a lack of estimates in different conditions, we did not vary survival or germination fractions by growing season conditions in our models.

Intrinsic growth rates and per-capita competition coefficients were parameterized for each focal species in each rainfall treatment separately using Bayesian methods with MCMC sampling in RStan v2.21 (Stan Development Team, 2020). Models were fit with 4 chains for 40,000–60,000 iterations and a thinning parameter of 3 until all estimates converged with an $\hat{R}$ of 1, using uninformed priors only constrained for biological feasibility ($\alpha \sim$ Normal(0,1); $\lambda \sim$ Gamma(0.001, 0.001); $\lambda \geq 0$). Posteriors were then qualitatively evaluated to ensure realistic fits and approximately normal distributions. See Appendix S2 for all estimated parameters and priors, and for modelling scripts.

2.4 | Invasion analysis

Once models were parameterized, we assessed the potential for coexistence among pairs of species with the mutual invasion criterion (Chesson, 2000). Briefly, two species meet the mutual invasion criterion if they each have positive low density growth rates (LDGR) when invading a community composed of the other resident species at equilibrium, that is if $\log\left(\frac{N_{x,t+1}}{N_{x,t}}\right) > 0$. If this is the case, then both species can increase when rare and stable coexistence is predicted. If neither species can successfully invade the other, then priority effects are expected such that the first species to establish will exclude the other. If only one species has a positive growth rate when rare, then it is assumed to be competitively dominant and will outcompete the other species.

We first compared pairwise coexistence within a single rainfall condition. To establish resident equilibrium communities, we simulated each species in each rainfall treatment in the absence of interspecific competitors (Equation 1) until their populations reached steady-state abundance. Then, to determine pairwise LDGR and thus the capacity for coexistence among species pairs in a given environmental condition, we invaded a single individual of each species into every permutation of resident competitor and rainfall treatment, and calculated their projected population growth rate (Equation 1). This was replicated 200 times, each time drawing parameter combinations from species' posterior distributions. In scenarios where invasibility was not found (negative or zero LDGR), we iteratively reduced resident population size until the invader had a positive LDGR, indicating the degree that a dominate competitor would need to be reduced for the inferior competitor to persist (Figure S2).

2.5 | Partitioning LDGR

To assess the degree to which variable rainfall environments altered LDGR, we first reconstructed historical rainfall conditions in the early growing season (fall) at Brown's Valley from 1896 to 2016 (PRISM Climate Group, OSU 2004; Hallett et al., 2019). Any year with precipitation from September to December less than the 50th percentile for that time span was considered a dry fall that is early dry, and any fall over the 50th percentile was considered a wet fall that is early wet. Using this time series, we estimated equilibrium resident abundance based on the average conditions and simulated pairwise invasions. Only the most recent 72 years of data were used for LDGR simulations to provide a sufficient time buffer (50 years) for resident populations to reach equilibrium.

To decompose the component coexistence mechanisms and estimate their contribution to coexistence or exclusion, we used this rainfall history in a simulation approach as described by Ellner et al. (2019). We decomposed the invader's average LDGR across variable rainfall conditions $\left(\bar{r}_i - \bar{r}_r\right)$, where $\overline{r_i}$ is the average invader LDGR growth rate under variable conditions and $\overline{r_r}$ is the average resident growth rate(0 at steady state), into four component values:

$$\overline{r_i} = \overline{r_i} - \overline{r_r} = \Delta_i^0 + \Delta_i^{\alpha} + \Delta_i^{\lambda} + \Delta_i^{\alpha\lambda} \tag{2}$$

Representing the contribution of variation-independent mechanisms to coexistence (i.e. when competition and intrinsic seed production were held constant at their mean values; Δ^0) and the contributions of variation-dependent mechanisms, namely the relative nonlinearity in per-capita competition (Δ^{α}), the relative nonlinearity in intrinsic seed production (Δ^{λ}), and the effect analogous to the temporal storage effect, plus the effect of the variance in environmental conditions per se ($\Delta^{\alpha\lambda}$, Ellner et al., 2019). Δ^0 is calculated as the invader LDGR minus the resident log growth rate under average environmental conditions: $\Delta^0 = r_i\left(\bar{\lambda}, \bar{\alpha}\right) - r_r\left(\bar{\lambda}, \bar{\alpha}\right)$. Because Δ^0 accounts for all effects unrelated to environmental variation, it represents intrinsic fitness differences between two competitors that is the difference in their LDGR under average competition and seed production parameters. Δ^{λ} and Δ^{α} are determined as the log growth rate subtracted from Δ^0 when either λ or α are allowed to vary with the environment respectively, while the other term is fixed to average conditions, for example $\Delta^{\lambda} = \left(r_i(\lambda, \bar{\alpha}) - r_r(\lambda, \bar{\alpha})\right) - \Delta^0$. Each quantifies the effect of environmental variation on either per-capita competition or seed production when the other is fixed. Finally, $\Delta^{\alpha\lambda}$ is calculated as the remainder of $\bar{r}_i - \bar{r}_r$ after subtracting out the other three components: $\Delta^{\alpha\lambda} = \bar{r}_i - \Delta_i^0 - \Delta_i^{\alpha} - \Delta_i^{\lambda}$. All terms are therefore calculated for both invader and resident in each pairwise invasion analysis, and the final partition associated with each mechanism is defined as the invader partition minus the resident $\overline{(r_i - \bar{r}_j)}$; while the resident's expected growth rate is near 0 and the values of $\bar{r}_i$ and $\bar{r}_i - \bar{r}_j$ are expected to be similar, the partitions of the resident's growth only sum to 0 and must be individually separated from invader partitions. All analyses were performed in R version 4.0.2 (R Core Team, 2020).

3 | RESULTS

3.1 | Coexistence

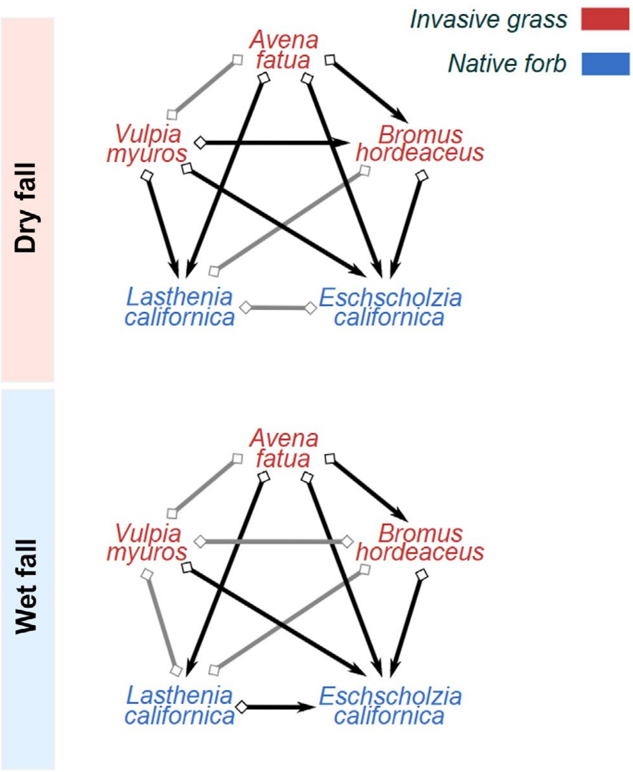

FIGURE 1 Invasibility diagram for all species pairs in both treatments. A directional arrow indicates that the originating species can invade the terminal species, while an open diamond indicates competitive exclusion. Black lines indicate one-sided invasibility, while grey lines indicate mutual competitive exclusion. Invasive grasses are in red text while native forbs are in blue text.

No species pair exhibited the potential for stable coexistence under a single rainfall condition (Figure 1). Instead, each species pair exhibited either mutual competitive exclusion (black connecting lines, Figure 1) or one-sided competitive dominance (mono-directional arrows in both treatments, Figure 1). A few species pairs exhibited invader LDGR very close to zero (e.g. *A. fatua* and *V. myuros*), indicating that even weak alternative sources of stabilization or greater rainfall variability could facilitate coexistence (see Figure S1 for all pairwise LDGR; Figure S2 for relative resident equilibrium communities necessary for invasion).

Early season rainfall conditions shifted competitive outcomes for most species, but still did not allow for any pairwise coexistence (Figure 1). Specifically, *V. myuros* was a more successful invader in early season dry treatments (invading all species except *A. fatua*), while *L. californica* was more successful at invading and resisting invasion in early season wet treatments (invading or exhibiting priority effects with all species except *A. fatua*; Figure 1). In contrast, *E. californica* was a weak competitor in both rainfall environments, but particularly under early season wet treatments, when it was incapable of successfully competing against any species (Figure 1). *B. hordeaceus* was generally competitively inferior to all species except *E. californica*, but under early season wet conditions it was able to maintain priority effects with two other species (Figure 1). The only species whose competitive outcomes were unaffected by rainfall conditions was *A. fatua*. It was the most successful competitor among the five by a significant margin and was able to invade every species in both treatments except for *V. myuros*, with which it exhibited priority effects (Figure 1).

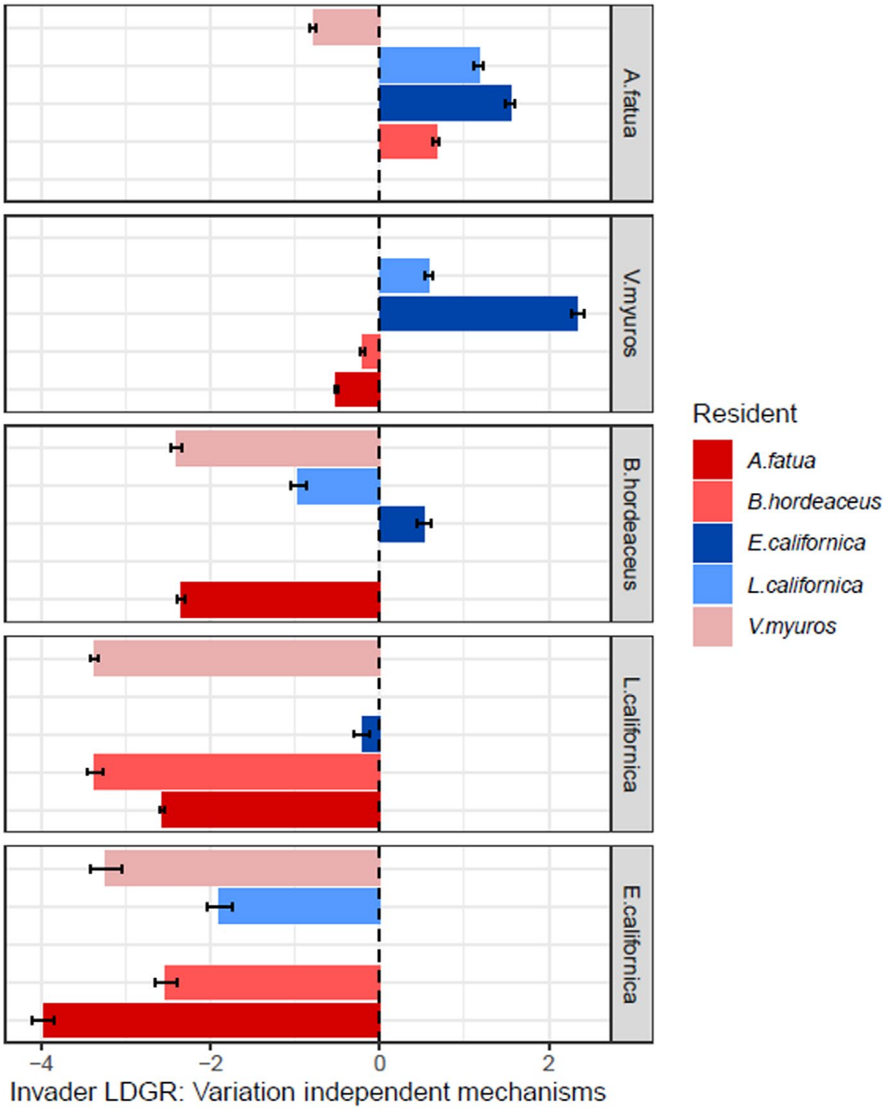

FIGURE 2 Variation-independent component (Δ^0) of log LDGR for each species as an invader competing with each other species as a resident. Negative values represent a destabilizing influence, and positive values a stabilizing influence. Blue bars are native forbs and red bars are non-native grasses. Error bars represent one standard deviation of the variation from propagating uncertainty in the posteriors bootstrapped partition elements.

3.2 | Mechanism partitioning

Partitioning LDGR into its component mechanisms revealed that the variation-independent component (Δ^0) was largely responsible for a lack of coexistence among most species. The average effect size of Δ^0 was overwhelmingly negative (−1.09 log LDGR ±0.43 SE, calculated across species pairs; Figures 2 and 3), implying that large intrinsic fitness differences given average environmental conditions were overwhelming other stabilizing mechanisms. The non-native grasses *A. fatua* and *V. myuros* were the only two species with positive Δ^0 on average (*A. fatua*: 0.89 log LDGR ±0.52 SE; *V. myuros*: 0.43 log LDGR ±0.67 SE; Figure 2), while all other species exhibited strong, negative Δ^0 (*B. hordeaceus*: −1.62 log LDGR ±0.72 SE; *L. californica*: −2.07 log LDGR ±0.67 SE; *E. californica*: −3.06 log LDGR ±0.47 SE).

Environmental variation from early season rainfall had a minor but net stabilizing effect in our experiment averaged across all species pairs ($\overline{\Delta}_i^{\alpha} + \overline{\Delta}_i^{\lambda} + \overline{\Delta}_i^{\alpha\lambda} = 0.092$ log LDGR). All of the stabilizing contribution came from the relative nonlinearity in competition Δ^{α} (0.14 log LDGR ±0.33 SE) and the interaction term associated with the storage effect $\Delta^{\alpha\lambda}$ (0.088 log LDGR ±0.28 SE), while there was a small negative contribution to invader LDGR from the relative nonlinearity in λ, Δ^{λ} (−0.14 log LDGR ±0.057 SE; Figure 3). However, the magnitudes of Δ^{α} and $\Delta^{\alpha\lambda}$ were considerably biased by a single species. *V. myuros* benefitted greatly from Δ^{α} (2.37 log LDGR ±0.058 SE), while hindered commensurately by $\Delta^{\alpha\lambda}$ (−1.61 log LDGR ±0.46 SE). When mechanisms are aggregated without *V. myuros* as an invader, the relative nonlinearity in competition Δ^{α} emerges as a destabilizing influence (−0.42 log LDGR ±0.22 SE) and the storage effect term as a meaningful stabilizing influence (0.51 log LDGR ±0.24 SE). Thus, relative nonlinearity was generally destabilizing and the storage effect was generally stabilizing, though this was strongly opposite for one species in the experiment, the most conservative grass (see functional PCA, Figure S10).

L. californica and *E. californica*, both native forbs unable to invade non-native grasses, exhibited similar responses to environmental variability. When invading *A. fatua* and *B. hordeaceus*, their variation-dependent partitions ($\overline{\Delta}_i^{\alpha} + \overline{\Delta}_i^{\lambda} + \overline{\Delta}_i^{\alpha\lambda}$) were very close to 0 (Figure 4), implying no benefit from environmental variability. When invading *V. myuros*, each experienced a stabilizing effect from the storage effect, but this was offset by equally negative partitions from the

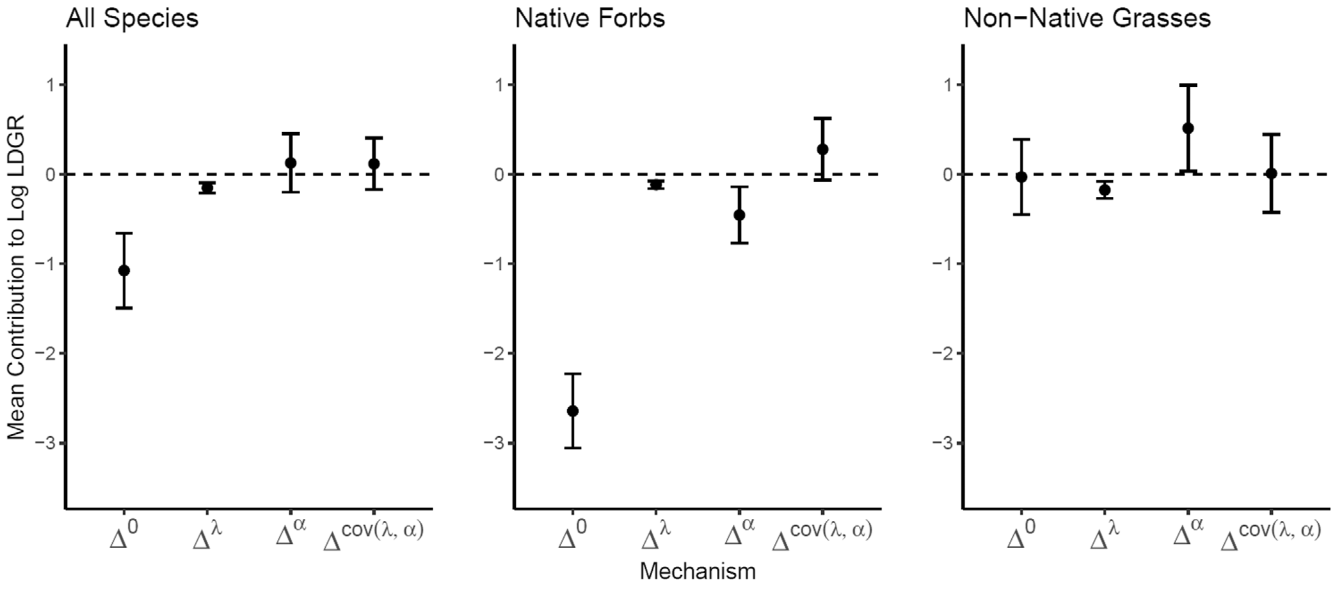

FIGURE 3 All coexistence partitions of log LDGR averaged across all species and treatments, just native forbs, and just non-native grasses. Negative values represent a destabilizing influence, and positive values a stabilizing influence. Error bars represent one standard error of the mean. Δ^0 represents variation-independent mechanisms; Δ^λ and Δ^α represent relative nonlinearity in the intrinsic growth rate or per-capita competition coefficients respectively; $\Delta^{\alpha\lambda}$ represents both the influence of environmental variation per se, as well as the covariance between the environmental benefit and strength of competition that is the temporal storage effect.

relative nonlinearity in competition ($\overline{\Delta_i^\alpha}$), washing out any stabilizing effect from environmental variation.

4 | DISCUSSION

California grasslands are simultaneously characterized by a legacy of successful invasions and frequent failure by native species to coexist with non-native species, as well as high rainfall variability, which is thought to facilitate coexistence of functionally distinct species (Dudney et al., 2017; Hallett et al., 2019; Pitt & Heady, 1978; Wainwright et al., 2019). By parameterizing annual plant population models from a competition experiment under ambient versus drought early season rainfall treatments, we were able to quantify the influence of rainfall variability on competition between five annual species with differences in provenance (native, non-native), functional group (forb, grass) and traits (acquisitive, conservative). Overall, we observed no coexistence among our five focal species, while one-sided competitive outcomes or mutual competitive exclusion was ubiquitous. Non-native annual grasses were particularly effective competitors, while native forbs were unable to sufficiently benefit from rainfall variability to overcome these large average fitness differences. Priority effects were common and mediated by rainfall, which may contribute to the highly variable species composition that characterizes the system. While rainfall variability had little to no effect on native forb growth rates, it shaped the success of the non-native grasses, with the most acquisitive grass, *A. fatua*, benefiting from a storage effect in wet years and the most conservative grass, *V. myuros*, benefiting from relative nonlinearity in competition with a competitive release in dry years. This suggests that rainfall variability does little to either enhance or offset average the fitness advantages that characterize non-native grass invasion, but that it has a role in maintaining the diversity of non-native grasses that now dominate the system.

4.1 | Coexistence and competitive exclusion

Most species were not capable of coexistence in our experiment. Specifically, competition was dominated by non-native annual grasses, namely *A. fatua* in both rainfall treatments and *V. myuros* in early season dry treatments. Our findings therefore suggest that *A. fatua* is competitively dominant, consistent with adjacent work demonstrating dominance by *A.* spp. in communities where present (Shaw et al., 2022). In contrast, native forbs were poor competitors averaged over rainfall conditions. Their variation-independent LDGR partitions were overwhelmingly negative, implying considerably lower fitness differences compared to *A. fatua* and *V. myuros*. Even though variation-dependent mechanisms were net positive, early season rainfall variability was not sufficient to overcome these fitness differences. Thus, the potential for rainfall variability in California grasslands to maintain coexistence through variation-dependent mechanisms (Bartolome, 1979; Hallett et al., 2019; Pitt & Heady, 1978) may be very minor for native forbs and is clearly neutered in the face of fitness advantages characteristic of non-native annual grass species.

California grasslands are often characterized as a 'non-equilibrium' system in which the combination of seed rain and climate variability make it difficult to predict species composition. Our study provides some additional mechanistic insight into this idea.

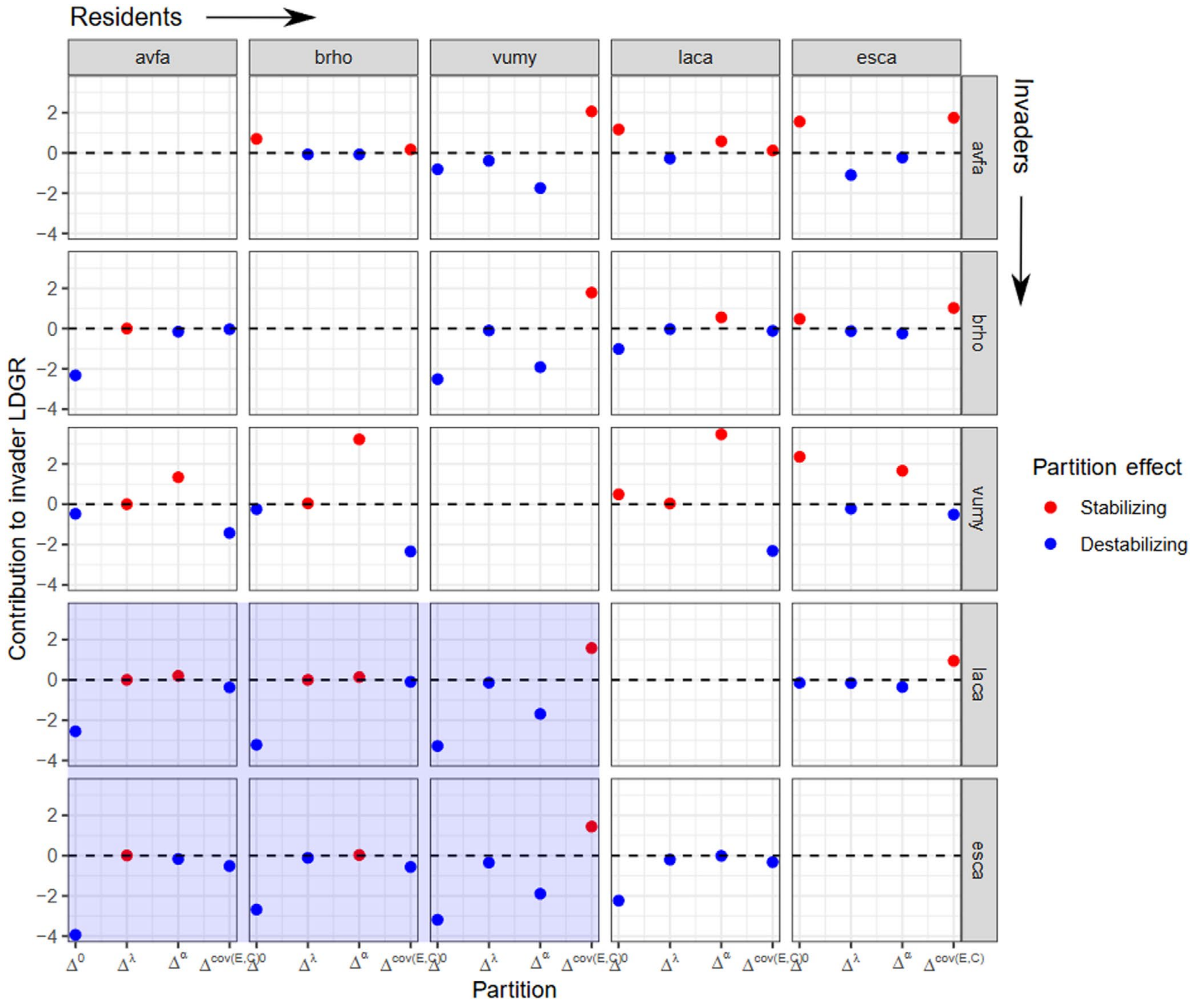

FIGURE 4 All coexistence partitions of log LDGR for each species as invader into each other species as resident. Negative values (blue) represent a destabilizing influence, and positive values (red) a stabilizing influence. Δ^0 represents variation-independent mechanisms; Δ^λ and Δ^α represent relative nonlinearity in the intrinsic growth rate or per-capita competition coefficients respectively; $\Delta^{\alpha\lambda}$ represents both the influence of environmental variation per se, as well as the covariance between the environmental benefit and strength of competition that is the temporal storage effect. Blue-shaded graphs are native forbs invading into non-native grasses. No error bars were included because the variation in LDGRs from propagating posterior uncertainty was too small to be meaningful on the figure. ‘avfa’ is *Avena fatua*, ‘brho’ is *Bromus hordeaceus*, ‘vumy’ is *Vulpia myuros*, ‘laca’ is *Lasthenia California*, and ‘esca’ is *Eschscholzia californica*.

First, multiple species pairs were unable to invade one another at equilibrium, indicated by mutual negative LDGRs. Thus, while there is some indication of a robust competitive hierarchy (e.g. *A. fatua*), the overall picture is more complicated. Rather, our results suggest that California grasslands are sensitive to priority effects, in which establishment success is partly a function of which species arrives at a site and grows first. Indeed, the potential for priority effects have been consistently identified in California grasslands (Bartolome & Gemill, 1981; Corbin & D'Antonio, 2004; Dickson et al., 2012), to which our study provides further support (but see Mordecai et al., 2015).

Second, early season rainfall conditions were still a major determinant of competitive outcomes. In particular, the success of both *V. myuros* and *L. californica* were sensitive to rainfall treatments, benefitting more from early season dry or wet conditions respectively. In conjunction with its net stabilizing influence, our results unsurprisingly support the notion that fall rainfall mediates community composition in California grasslands. The only species whose competitive outcomes were completely insensitive to early season rainfall was *A. fatua*. It is likely that other factors are necessary to control such competitively dominant species. Top-down factors like fire or seed predation are a possibility, though *A. fatua* is highly disease resistant (Loskutov & Rines, 2011) as well as an effective pest reservoir with a consequently negative effect on competitors (Power & Mitchell, 2004). Even when *A. fatua* was reduced to 50% of resident equilibrium abundance, *V. myuros* was the only species that could successfully invade (Figures S2 and S3), emphasizing its strong competitive effect, even across variable densities.

It is worth emphasizing that greater variability than we generated in our experiment could strengthen the potential for rainfall to maintain diversity. While our rainfall exclusion treatments were effective, the growing season of the experiment was wetter than average (67th percentile in rainfall). Our dry treatment was therefore representative of a typical dry year (23rd percentile in rainfall) rather than a very dry year. This may further explain why *A. fatua* was highly successful even in the early season dry treatment. It is possible that the more conservative species in our experiment could be more competitive than observed in our experimental early season dry conditions. Furthermore, we did not vary germination rates with rainfall treatment in our models. If species-specific germination rates were consistent with their growth niches, germination rates varied widely with rainfall, and seed survival rates remained otherwise consistent, then the temporal niche would strengthen. Specifically, less competitive species (native forbs) could avoid competition with more competitive species (non-native grasses) by germinating less under conditions favourable for more competitive species (Levine & Rees, 2004). However, given *A. fatua's* success in drier conditions, this stabilizing effect would be limited in scope.

4.2 | Coexistence partitioning

Partitioning of coexistence mechanisms revealed multiple salient outcomes: that rainfall variation had a small net stabilizing effect on coexistence on average, that this variation helped non-native grasses but not native forbs, and that this effect was overwhelmed by the destabilizing influence of variation-independent fitness differences. Specifically, the variation-independent component of LDGR (Δ^0) was negative for most species in the experiment (Figure 2). Δ^0 represents at once both density-dependent responses to resource availability and predation, as well as intrinsic fitness differences averaged over environmental variation. We therefore conclude that large average fitness differences are precluding coexistence between most species pairs in our experiment, and benefitting non-native annual grasses in particular. In this way our study develops previous studies in the same or similar systems finding a failure of coexistence among commonly co-occuring species (Kraft et al., 2015; Van Dyke et al., 2022; Wainwright et al., 2019), where we conclude that rainfall variability is insufficient to explain this discrepancy. Future studies should examine other possible sources of stabilization for example, top-down factors like grazing or disease intensity.

More importantly, early season rainfall variation was not sufficient to facilitate stable coexistence in the face of these variation-independent fitness differences (Figure 3). For four of our five species, the partitions associated with relative nonlinearity in competition and intrinsic seed production that is Δ^α and Δ^λ, destabilized invader LDGR on average (Figures S4–S9), while the term associated with the temporal storage effect that is $\Delta^{\alpha\lambda}$ was slightly stabilizing. Native forbs in particular had little to no benefit at low densities from rainfall variation, while non-native grasses often benefitted at low densities (Figure 4), implying weaker temporal niches in the former and strong niches in the latter. In a similar prior study, albeit conducted in a drought year, variation-dependent mechanisms had meaningful stabilizing effects in non-native forb (*Erodium botrys*) and grass (*Avena barbata*) competition (Hallett et al., 2019), both native to Eurasian and Mediterranean grasslands. These functionally disparate species therefore appear to have better partitioned rainfall niches compared to the native forbs and non-native grasses. This could reflect a lack of co-evolutionary history between native forbs and non-native grasses in California grasslands; because the stabilizing effects of variable environments stem from distinct functional response curves between competitors or from different degrees of self-limitation in favourable environments (Chesson, 2000), co-evolved species may be more likely to differently benefit from favourable environmental conditions more than they are limited by unfavourable conditions.

Notably, *V. myuros* exhibited qualitatively different responses from the other four species. The storage effect was weakly stabilizing for three species (*A. fatua*, *B. hordeaceus* and *L. californica*) and irrelevant for *E. californica*, while relative nonlinearity was destabilizing for these same species. *V. myuros* instead benefitted considerably from relative nonlinearity in competition, while the storage effect was destabilizing, suggesting that its competitive strength was significantly mediated by favourable environments. This is evident in the variability of its competitor's pairwise competition coefficients with *V. myuros* across treatments, which are an order of magnitude lower in dry treatments (see Appendix S2). This difference is much smaller for the other species. These disparate effects of rainfall treatment align with functional trade-offs: *A. fatua*, *B. hordeaceus* and *L. californica* are more resource-acquisitive (citation), while *V. myuros* is generally resource-conservative (Figure S10; Butterfield & Suding, 2013). Thus, the ability to tolerate dry environments accompanied a high degree of competitive release in drier conditions. Speculatively, this could reflect an asymmetry in how different resource environments affect different functional groups. Resource-conservative species tolerate drier conditions but also still benefit from wetter conditions, leading to less interspecific competition in dry years (stabilizing) but more interspecific *and* intraspecific competition in wetter years (negative E-C covariance; destabilizing). In contrast, resource-acquisitive species benefit greatly as invaders in wetter conditions, and thus have more to gain via seed storage until more favourable conditions, enhancing the importance of the storage effect. Competition experiments with other functionally distinct grass species in varying wet and dry environments could reveal whether this association between resource use and stabilizing mechanisms is more general.

Finally, the temporal storage effect is commonly cited as an important driver of coexistence in plant communities (Adler et al., 2006; Angert et al., 2009; Pake & Venable, 1995; Stump & Vasseur, 2023).

Our results provide support for this idea, though it was also destabilizing or irrelevant in some competitive contexts. Our study is the second recently to find a weak or destabilizing influence of the temporal storage effect at the same site (see Hallett et al., 2019). It is therefore worth considering whether this is especially surprising for annual plants. For a strong temporal storage effect to operate in such systems, early season germination conditions (e.g. fall rainfall) must also be highly correlated with conditions later in the growing season (e.g. winter and spring rainfall), assuming overlap between germination and growth niches. If the environment is highly variable, then the conditions that favour the germination of one set of competitors may disfavour those competitors later on, weakening the Environment-Competition covariance that drives the storage effect. Indeed, early (Sep–Dec) and late (Feb–Apr) growing season rainfall are effectively uncorrelated at Browns Valley ($\rho = -0.028$; 1986–2016), suggesting a weak E-C covariance at our site. Alternatively, $\Delta^{\alpha\lambda}$ could be weakened if there was a negative E-C covariance, potentially due to asymmetry in germination between competitors (Holt & Chesson, 2014). Ultimately, more replication in annual systems outside of California is warranted. However, an accessible method for partitioning such mechanisms (Ellner et al., 2019) has only been available for a few years, and more wide application of this process may reveal that this is more general in grasslands than may have been assumed.

5 | CONCLUSIONS

Taken together, our results suggest that early season rainfall variation of the magnitude we observed is not sufficient for stable coexistence among native and non-native species in California grasslands. The influence of rainfall variation and variation-dependent mechanisms of coexistence was dwarfed by average variation-independent fitness differences between species, suggesting that better adaptation to rainfall conditions is a primary mechanism of non-native grass invasiveness. Thus, for stable coexistence to be expected, other forms of environmental heterogeneity, such as stronger rainfall variation, or other density-dependent factors like predation must come into play. Some non-native species in California grasslands therefore appear to require multiple limiting factors in the environment if natives are to remain competitive. With respect to the mechanisms at play, variation-dependent mechanisms were just as likely to stabilize as destabilize coexistence. These findings suggest that early season rainfall variation may not be an especially relevant driver of coexistence among competing native grasses and non-native forbs in this system. However, our results do suggest that the influence of temporal variation may differ along functional axes of resource use (Van Dyke et al., 2022; Wainwright et al., 2019). Further work is warranted in generalizing these findings to other annual plant systems and exploring the potential reasons why the temporal storage effect, long considered a key variation-dependent stabilizing mechanism, was unimportant to coexistence in California grasslands in our study.

AUTHOR CONTRIBUTIONS

Andrew J. Muehleisen and Caitlin T. White contributed equally to the development of this study. All authors conceived and conceptualized initial questions for this study. Caitlin T. White and Katharine N. Suding conceived of and implemented the field experiment, and Caitlin T. White was responsible for field work/data collection. Andrew J. Muehleisen and Lauren M. Hallett wrote the manuscript and implemented data analyses, with code initially supplied by Lauren S. Shoemaker. All authors contributed extensive writing feedback, section edits and methods feedback to the manuscript.

ACKNOWLEDGEMENTS

Research was supported by USDA-NIFA grant #2014-67019-21613. We thank Vivian White for assistance with seed collection and the research and administrative staff at Sierra Foothill Research and Extension Center for assistance with project implementation, especially Nikolai Schweitzer and Mike Williams for their help installing the experiment and collecting data at the field site. We also thank Austin Willbern and Anoushka Singh for their many hours of assistance processing samples. L.S.S. was supported by NSF award #EPS-2019528 and L.M.H. was supported by NSF award #2047239.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14451.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j3tx95xqk (Muehleisen et al., 2024).

ORCID

Andrew J. Muehleisen https://orcid.org/0000-0003-1389-5643
Caitlin T. White https://orcid.org/0000-0001-8723-3568
Lauren S. Shoemaker https://orcid.org/0000-0002-4465-8432
Katharine N. Suding https://orcid.org/0000-0002-5357-0176
E. Ashley Shaw Adams https://orcid.org/0000-0002-4768-3465
Lauren M. Hallett https://orcid.org/0000-0002-0718-0257

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SUPPORTING INFORMATION

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

Appendix S1. Figure S1. Log low-density growth rates (LDGR) for every pair of species in both treatments.

Figure S2. The proportion of each resident's equilibrium carrying capacity at which each invader (row-wise facets) has a positive LDGR.

Figure S3. Invasibility diagram for all species pairs in both treatments, but resident species are at 50% equilibrium.

Figures S4–S8. All coexistence partitions of log LDGR averaged for each species.

Figure S9. All coexistence partitions of log LDGR, averaged across species and treatments excluding *V. myuros*.

Figure S10. Principal components analysis of functional traits for *A. fatua*, *B. hordeaceus*, and *V. myruros*.

Figure S11. Sensitivity of the LDGR partitions to all possible values of seed survival, *s*, for *A. fatua*.

Figure S12. Sensitivity of the LDGR partitions to all possible values of seed germination, *g*, for A. *fatua*.

Appendix S2. Table S1. Absolute values of parameter estimates for each species in each treatment.

Table S2. Competition coefficients scaled by λ, so that they represent per-capita impact on fecundity as a percentage (more directly comparable across species and treatments).

Appendix S3. Photos of the experiment.

Appendix S4. Table: Seeding densities for each species in each treatment.

Appendix S5. Seed bank references.

Appendix S6. Allometric relationships.

Appendix S7. Example code for all analyses. All code is in R, except for the Stan model which is in C.

Appendix S8. Soil moisture data from the study's growing season (September–April) collected in wet treatments (blue) and in dry rainout shelter treatments (red).

How to cite this article: Muehleisen, A. J., White, C. T., Shoemaker, L. S., Suding, K. N., Adams, E. A. S., & Hallett, L. M. (2025). Fitness differences override variation-dependent coexistence mechanisms in California grasslands. *Journal of Ecology*, *113*, 194–205. https://doi.org/10.1111/1365-2745.14451