

Fluctuation-dependent coexistence of stage-structured species

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Abstract

Modern coexistence theory is a dominant framework for understanding how environmental fluctuations promote species coexistence. However, quantifications of fluctuation-dependent mechanisms of coexistence, such as the storage effect, are predominantly based on annual systems, despite the global prevalence of mixed annual-perennial ecosystems. This has impeded our ability to bridge from theory to empirical studies and to generalize our current understanding of how environmental variability and species interactions jointly alter coexistence. Here, we use models of perennial, annual seedbanking, and annual non-seedbanking species to explore how mechanisms of coexistence vary between annual and perennial systems across three scenarios, representing resource partitioning, water-limitation, and light/space-limitation. We show that fluctuation-dependent mechanisms of coexistence can be equally important in coexistence patterns for perennial species with an adult “storage” stage, as for seedbanking annuals. Further, we find that assumptions about the role of species interactions from annual models may overlook the role of the storage effect when the perennial species is the resident competitor, due to adults exerting competitive pressure during non-favorable years. This work sets the stage for applying coexistence theory and fluctuation-dependent partitioning frameworks to perennial and mixed stage-structure communities, facilitating understanding of how environmental variation drives species dynamics beyond annual plant systems.

Introduction

Fluctuations in the environment, species interactions, and their joint effect fundamentally structure population and community dynamics, from species growth to coexistence and the maintenance of biodiversity. While the importance of environmental fluctuations and species interactions in maintaining biodiversity has long been recognized, dating back to definitions of the niche (Carscadden et al., 2020; Elton, 1927; Vandermeer, 1972), more recent formalization via the modern coexistence theory framework provides an opportunity to partition when and how fluctuations in the environment versus species interactions maintain biodiversity (Chesson, 2000*b*). However, the mathematics required to partition fluctuation-dependent coexistence mechanisms (Chesson, 2000*b*) have largely limited its applications to annual plant systems that can be described with relatively simple mathematical models that allow for analytical solutions. This has stymied our ability to make inferences about the joint effects of environmental variability and competition in structuring diversity across different ecosystem types and in more complex communities. Extending the modern coexistence framework both conceptually and analytically to reflect systems with mixed growth forms is essential to understanding most empirical systems.

In the modern coexistence theory framework, species are determined to coexist if they have positive low-density growth rates when other species are present at equilibrium (Barabás et al., 2018; Chesson, 2000*b*; Grainger et al., 2019). This low-density growth rate is then partitioned into multiple fluctuation-dependent mechanisms which can increase or decrease the likelihood of coexistence (Chesson, 1994, 2000*a*; Shoemaker and Melbourne, 2016). For example, the storage effect is the most commonly considered fluctuation-dependent mechanism of coexistence and quantifies the joint effect of environmental fluctuations and competitive environments. Coexistence is promoted via the storage effect if (1) species partition environmental variation, (2) periods with beneficial environmental conditions correspond with periods of reduced competition or increased facilitation (i.e. the covariance between the environment and competition) and (3) species exhibit an ability to “store” the positive effects of good years (i.e. buffered growth),

such as through bet-hedging and seed banks (Sears and Chesson 2007; Stump and Vasseur 2023, but see Johnson et al. 2023). In addition, environmental variability can promote coexistence due to relative nonlinearity, in which the positive growth response of species to “good” years is relatively larger than their negative response to “bad” (Barabás et al., 2018; Letten et al., 2018), owing either to direct environmental response or competitive release (Ellner et al., 2019). Given that most tests of modern coexistence theory are in annual systems, the storage effect is most commonly equated with seed banking in annual plants (Angert et al., 2009; Sears and Chesson, 2007), despite its generality to dormancy (Cáceres, 1997; Wisnoski and Lennon, 2021) and storage more generally (Johnson and Hastings, 2022).

Perennial species represent a key facet to understanding and quantifying fluctuation-dependent mechanisms within the modern coexistence framework, through their role is under-explored compared to annual plants (but see Adler et al., 2006; Chu and Adler, 2015; Usinowicz et al., 2012). This is somewhat surprising, as other analytical approaches, such as matrix and integral projection models (IPMs), have long highlighted the importance of variable environmental conditions for the persistence of perennial species (Dahlgren and Ehrlén, 2009; Doak et al., 2021; Verhulst et al., 2008; Yang et al., 2022). Additionally, across perennial systems environmental variation has been shown to have substantial indirect impacts via species interactions, sometimes outweighing direct impacts of environmental change on species’ persistence and community dynamics (Collins et al., 2022; Paniw et al., 2023; Usinowicz and Levine, 2021). The stage-structured life history of perennial species includes a buffering stage, with many adults less sensitive to “bad” environmental conditions and less impacted by competitors. As such, recruitment stages and demographic transitions of germination and early survival are often more impacted by abiotic- and biotic context, and potentially more important determinants of coexistence in perennial systems (Chu and Adler, 2015; Lyu and Alexander, 2023). Additionally, the adult perennial buffering stage contrasts with buffering from seed banks for annual species, as it contributes to intraspecific density-dependence as well as interspecific competitive interactions (Adler et al., 2006). The potential impact of this key difference in buffering stage on patterns of

72 coexistence and the strength of fluctuation-dependent mechanisms including the storage effect
has not yet been explored.

Further, many ecological communities have multiple coexisting life history strategies, such as
75 mixed perennial-annual communities. In fact, differing life history strategies can be an important
axis of differentiation for coexistence, and stage-structured species may differ in their sensitivity
to environmental fluctuations (Cleland et al., 2013; Jops and O'Dwyer, 2023). Extending coexis-
78 tence models to interacting species with different stage-structured life history strategies would
broaden our understanding of the impacts of environmental fluctuations on these communities,
and enable us to better generalize current conclusions drawn from annual systems about the
81 relative strengths and importance of different fluctuation-dependent mechanisms for coexistence
and community dynamics. Critically, the strengths and impacts of fluctuation-dependent mech-
anisms of coexistence likely also depend on the broader ecological context. For example, at a
84 site with fluctuating precipitation, species' competitive strengths might be higher in wet years, if
light and space are limiting factors, or alternatively in dry years if water is a limiting factor. De-
composing mechanisms of coexistence in these different scenarios—whether nutrients, water, or
87 space/light are limiting—will inform the structure and stability of pairwise species coexistence.

More recent simulation-based approaches (Ellner et al., 2019) have extended from classic
modern coexistence theory to explicitly quantify how environmental fluctuations impact demo-
90 graphic rates and competitive environments, and thus alter coexistence. This flexibility supports
the empirical application of modern coexistence theory, both in annual plant (Aoyama et al.,
2022; Hallett et al., 2019) and other systems, such as yeast communities (Letten et al., 2018),
93 plant-soil feedbacks (Kandlikar et al., 2019; Ke and Wan, 2020), and predator prey systems (Shoe-
maker et al., 2020). These recent studies highlight how fluctuation-dependent mechanisms of
coexistence are ubiquitous across systems (e.g. Arnold et al. 2023; Jiang and Morin 2007; Sieben
96 et al. 2022). Additionally, they indicate that relative nonlinearity, which has historically been less
studied than the storage effect, often has stronger stabilizing effects for coexistence (Hallett et al.,
2019; Letten et al., 2018; Stump and Vasseur, 2023). Despite the broad and growing application of

simulation-based approaches, and the insights they have yielded, to date applications have still focus primarily on the coexistence of annual organisms.

Here we compare how fluctuation-dependent mechanisms impact dynamics for species with two different buffering life history stages: (1.) annual species with a soil seedbank and (2.) perennial species, with a potentially buffering adult life stage. We examine coexistence and the role of fluctuation-dependent mechanisms in three scenarios, each of which represents a different potential limiting resource. To do so, we extend the Ellner et. al. (2019) simulation approach for coexistence to mixed communities of annual and perennial species. To compare fluctuation-dependent mechanisms of coexistence between seedbanking annuals versus perennials, we paired each of these stage-structured species with a non-seedbanking annual species. We quantify coexistence mechanisms across different life history types using simulations and investigate how these vary with the patterns of environmental variation. We show that fluctuation-dependent mechanisms of coexistence in general, and the storage effect in particular, can be equally important in coexistence patterns for communities with perennial species, with an adult “storage” stage, as for seedbanking annual species. Further, invasion dynamics are mediated in perennial systems due to competitive effects from perennial-adults. Our work demonstrates how simulation-based approaches to modern coexistence theory can bridge from theory to empirical applications, as most systems are mixed annual and perennial. It provides a mathematical framework that can be applied to a variety of empirical perennial and mixed systems to better understand the impacts of environmental variation and species interactions on coexistence dynamics in communities with diverse life-history strategies.

Methods

To contrast the role of fluctuating-dependent mechanisms for coexistence in annual versus mixed communities, we first create dynamical population growth models for a baseline non-seedbanking annual, a seedbanking annual, and a perennial. Using our dynamical models, we quantify coex-

istence and the role of fluctation-dependent mechanisms, comparing two-species cases between the non-seedbanking annual and either (a) the perennial or (b) the seedbanking annual. We
 126 examine coexistence across three different environmental scenarios, representing cases where nutrients are limiting, water is limiting, and light/space is limiting.

Modeling Population Dynamics in Mixed Communities

Annual Community Models: We highlight patterns of coexistence and the role of the environ-
 mental variation in species with two different stage-structured life histories: annual species with
 a soil seedbank, and perennial species. To determine how these buffering life stages (one as
 132 seeds, the other as adults) impact coexistence, we simulate each of these species interacting with
 a non-seedbanking annual species as a baseline comparison. For all species, we use two-species
 discrete time competition models, building from the Beverton-Holt competition functions (Bever-
 135 ton and Holt, 1957) given their previous use in coexistence theory (e.g. Godoy and Levine 2014;
 Hallett et al. 2019; Levine and HilleRisLambers 2009. We focus on pairwise species interactions to
 facilitate comparisons across species life-history strategies and to avoid more complex situations,
 138 such as higher-order interactions (Kleinhesselink et al., 2022; Mayfield and Stouffer, 2017).

We model the population growth of the non-seedbanking annual species as:

$$N_{a,t+1} = \frac{N_{a,t}g_{a,t}f_{a,t}}{1 + \alpha_{aa,t}g_{a,t}N_{a,t} + \alpha_{ab,t}g_{b,t}N_{b,t}} \quad (1)$$

where a denotes the non-seedbanking annual, and b denotes the seedbanking annual. $N_{a,t}$ is the
 141 number of seeds of species a at time t , $g_{a,t}$ is the fraction of seeds of species a that germinate
 at time t , and $f_{a,t}$ is the number of seeds produced per individual of species a at time t in the
 absence of intra- or inter-specific competition. $\alpha_{aa,t}$ is the per-capita intraspecific competitive
 144 effect at time t and $\alpha_{ab,t}$ is the per-capita interspecific competitive effect of species b on species a
 at time t .

We expand on eqn. 1 to model the population growth of the seedbanking annual species, as:

$$N_{b,t+1} = d_b(1 - g_{b,t})N_{b,t} + \frac{N_{b,t}g_{b,t}f_{b,t}}{1 + \alpha_{ba,t}g_{b,t}N_{a,t} + \alpha_{bb,t}g_{b,t}N_{b,t}}, \quad (2)$$

147 with an additional first term in the equation to represent the persistent seeds in the seedbank,
where d_b is the survival of seeds of species b in the seedbank.

150 **Mixed Annual and Perennial Community Models:** To model perennial species populations, we
used a simple stage-structured model, where we consider dynamics of perennial seeds/seedlings
(0-1 year) and adults (1+ year) based on the model of Mordecai et al. (2015). We note that this
153 could be extended to more stages or even incorporate integral projection models when fitting
models to empirical data (Ellner and Rees, 2006; Merow et al., 2014).

First, the non-seedbanking annual population dynamics are modified from eqn. 1 when
156 competing with a perennial such that:

$$N_{a,t+1} = \frac{N_{a,t}g_{a,t}f_{a,t}}{1 + \alpha_{aa,t}g_{a,t}N_{a,t} + \alpha_{ap,t}g_{p,t}N_{p,t} + \alpha_{aP,t}N_{P,t}} \quad (3)$$

where p denotes the number of perennial seeds at time t and P is the number of 1+ year-old
adult individuals of the perennial species. As such, the annual now competes with both seedlings
159 (i.e. $g_{p,t}N_{p,t}$) and adults of the perennial species.

We model the perennial species as having two life stages (seeds/seedlings and adults) using
two paired equations to mostly closely mirror the life stage structure of the seedbanking annual.
162 The equation for the seed stage is:

$$N_{p,t+1} = \frac{N_{P,t}f_{P,t}}{1 + \alpha_{pa,t}g_{a,t}N_{a,t} + \alpha_{pp,t}g_{p,t}N_{p,t} + \alpha_{PP,t}N_{P,t}} \quad (4)$$

where p is the number of seeds at time t , P is the number of 1+ year-old adults at time t , and
 $f_{P,t}$ is the number of seeds produced by each adult P at time t . We assume that intra- and inter-
165 specific competition (α terms) affect the per-capita fecundity of the adults P . Finally, the equation
for the adult stage is:

$$N_{P,t+1} = N_{P,t}s_{P,t} + \frac{N_{p,t}g_{p,t}s_{p,t}}{1 + \alpha_{pa,t}g_{a,t}N_{a,t} + \alpha_{pp,t}g_{p,t}N_{p,t} + \alpha_{pP,t}N_{P,t}} \quad (5)$$

The first term represents the persistent adults in the population, where $s_{P,t}$ is the per-capita survival rate of adults P at time t . The second term represents the recruitment of seeds into the adult stage, where $g_{p,t}$ is the germination rate of seeds at time t and $s_{p,t}$ represents the survival of those germinated seeds to the next year. We assume that intra- and inter-specific competition (α terms) affect the survival of seedlings p , but not the survival of adults P due to size differences; however, this could be modified dependent on the systems and questions.

Quantifying persistence and coexistence using low density growth rate

Using our dynamical population models, we first quantify pairwise coexistence using the mutual invasion criterion, with the invader-resident comparison (Ellner et al., 2019; Hallett et al., 2019). In this framework, coexistence occurs when both species have positive average growth rates when “invading” into the other species at equilibrium (low-density growth rate, or ldgr, Barabás et al. 2018; Chesson 2000b; Grainger et al. 2019). Alternatively, if a species has a negative low density growth rate, it is predicted to be competitively excluded by the other.

To calculate ldgr we first simulated the “resident species” to equilibrium. To do so, we simulated the dynamical model for 200 time-steps (i.e. years) starting from an initial population size of 100, but with the invader species set to a population size of 0. When either of the annuals was the resident, this yielded their equilibrium abundances in the absence of interspecific competition. When the perennial was the resident, this yielded its equilibrium stage-structure and abundance.

We next, simulated an invasion of a single individual of the second species into the resident at equilibrium. We calculate growth rate of the invader at a given time t as:

$$r_i = \ln\left(\frac{N_{i,t+1}}{N_{i,t}}\right) \quad (6)$$

For the annual plants, we invaded a single seed into the resident species. For the perennial,

189 we needed to additionally determine the stage-structure equilibrium for the invading individual
 (mirroring spatial coexistence invasions, e.g. Shoemaker and Melbourne 2016). We did so by
 simulating a temporary invasion with a given stage structure ratio of seeds:adults. We compared
 192 the stage structure of the invading perennial at time t to $t + 1$. We updated the stage structure
 based on the simulation, normalizing to maintain an invading population size of one. We re-
 peated this process until the change in life stage ratio was less than or equal to 0.01, and then
 195 used this final equilibrium stage structure of the invader to calculate its growth rate r_i for all
 coexistence calculations.

For the invader (i)-resident (r) comparison, overall average ldgr was determined as:

$$ldgr = \bar{r}_i - \bar{r}_r. \quad (7)$$

198 where the bar denotes the average. We determined the resident's growth rate r_r with the invader
 present at each time step by dividing by its population size the timestep previously. Because the
 resident is at equilibrium, its average growth rate, $\bar{r}_r \approx 0$; however we include this comparison
 201 for the below decomposition of coexistence mechanisms. We repeated this invasion process
 process 100 times per invader-resident combination to determine the average ldgr in a given
 environment.

204 *Quantifying Mechanisms of Coexistence*

To determine how variation in environmental conditions mediates pairwise coexistence in annual
 versus mixed-communities (Fig 1A and B) via direct environmental responses, species interac-
 207 tions, or their combined effect, we employ the simulation-based approach of Ellner et al. 2019.
 We partition the low density growth rate (ldgr) such that:

$$\bar{r}_i - \bar{r}_r = \Delta_i^0 + \Delta_i^\lambda + \Delta_i^\alpha + \Delta_i^{\lambda\alpha} \quad (8)$$

where Δ_i^0 is the difference in average growth rates between the invader and resident under con-

stant, averaged environmental conditions. Δ_i^0 is calculated as the growth rate of the invader minus resident when all parameters are kept constant at their weighted average of the environmental time series. Δ_i^λ is the relative nonlinearity in species direct, demographic responses to environmental variation via seed production, germination, and survival. Δ_i^α is the relative nonlinearity in species interactions and quantifies the indirect effect of environmental variation on competitive interactions. Finally, the last term, $\Delta_i^{\lambda\alpha}$ is the interaction effect and quantifies the effects of variation that simultaneously impact competition and demography that are not accounted for by the combination of Δ_i^λ and Δ_i^α alone (Fig 1F) (Aoyama et al., 2022; Ellner et al., 2019; Hallett et al., 2019).

To assess generalized patterns of the role of environmental variation in coexistence, we simulated time series composed of two environmental conditions, X and Y. We conducted the partitioning in equation 8 by repeating the simulation for each time series and allowing different components of parameters to vary. Consistent with Ellner et al. (2019), the full $ldgr$ is calculated as $\bar{r}_i - \bar{r}_r$ with all parameters varying with the environment, where \bar{r}_i and \bar{r}_r are the averages of the invader and resident growth rates as defined in equation 7. Δ_i^0 is calculated with all parameters constant at their weighted average of the time series environments. We calculated Δ_i^λ as $\bar{r}_i - \bar{r}_r$ with only seed production λ , germination rates g and survival rates d and s varying with environment and all α terms constant at their weighted average, minus the nonvarying component Δ_i^0 . Δ_i^α is the complement of this, with only α terms varying with environment, minus Δ_i^0 . $\Delta_i^{\lambda\alpha}$ is simply $ldgr - \Delta_i^0 - \Delta_i^\lambda - \Delta_i^\alpha$ and requires no additional simulations.

Although the interaction term $\Delta_i^{\lambda\alpha}$ is roughly used as the quantification of the storage effect in this simulation-based approach, it differs slightly from the traditional, analytical concept of the storage effect as defined by Chesson (2000b). To assess whether the simpler to quantify interaction term $\Delta_i^{\lambda\alpha}$ is a sufficient approximation, we further partitioned $\Delta_i^{\lambda\alpha}$ into two components: the true storage effect $\Delta_i^{(\lambda\alpha)}$, and the remainder $\Delta_i^{\lambda \neq \alpha}$, which quantifies the interaction effect of variance in λ and α when the covariance is removed (Fig 1F). To do this, we repeat the simulation with the order of environmental conditions in the originally time series independently randomized

for direct environmental effect terms (λ , g , d , and s) and for α terms. $\Delta_i^{\lambda \neq \alpha}$ is calculated as the resulting no-covariance growth rate $(\bar{r}_i - \bar{r}_r) - \Delta_i^0 - \Delta_i^\lambda - \Delta_i^\alpha$. The effect of covariance between λ and α , i.e. the storage effect, can then be quantified as $\Delta_i^{(\lambda\alpha)} = \Delta_i^{\lambda\alpha} - \Delta_i^{\lambda \neq \alpha}$. This method is most closely comparable to the partitions in the chemostat example in Ellner et al. (2019). Our final resulting partition is:

$$ldgr = \Delta_i^0 + \Delta_i^\lambda + \Delta_i^\alpha + \Delta_i^{(\lambda\alpha)} + \Delta_i^{(\lambda \neq \alpha)} \quad (9)$$

Environmental Scenarios

We compare coexistence and its mechanistic contributions across three environmental scenarios, each motivated by different limiting factors that structure community dynamics (Fig 1C-E). For each scenario we compare ldgr for either the perennial or seedbanking annual invading the non-seedbanking annual or vice versa. As described above, each environmental scenario has two discrete environmental conditions that species experience through time. However, the overall framework would be equally applicable to more detailed environmental scenarios with more than two conditions (Hallett et al., 2019) or even continuous environmental variation (Weiss-Lehman et al., 2022). In each scenario, described below, we examine a gradient ranging from 100% environmental condition 1 to 100% environmental condition 2, calculating coexistence for every 0.05 increment of environment 1:environment 2 ratios. We ran 100 replicate simulations for each environmental ratio, for each species, and for each of the three environmental scenarios, for a total of 12,600 reciprocal invasion simulations. We explore different scenarios by varying the terms in our population growth models. In all scenarios, we assume that the competitive effect of perennial seedlings on perennial adults $\alpha_{p,p,t}$ is small enough to be negligible and, as such, we set this competitive term to zero.

Scenario 1, Different limiting nutrients: When two species are limited by different nutrients, we assume that opposite environments are favorable for each species' intrinsic growth rates and

each species exerts stronger inter- and intra-specific competition in its favorable environment (Fig 1C). This corresponds to species having different preferences or requirements for nutrient compositions, where nutrient concentrations fluctuate through time via temporal inputs. In the simulations between the non-seedbanking annual and the seedbanking annual species (Fig 1A), the non-seedbanking annual species' fecundity term $\lambda_{a,t}$ and its competitive rates $\alpha_{aa,t}$ and $\alpha_{ba,t}$ are higher in environment one, while the seedbanking species' fecundity term $\lambda_{b,t}$, germination term $g_{b,t}$, and competitive rates $\alpha_{ab,t}$ and $\alpha_{bb,t}$ are higher in the other environment. Similarly, in the simulations between the non-seedbanking annual and the perennial species Fig(1B), the non-seedbanking annual species' fecundity term $\lambda_{a,t}$ and its competitive rates $\alpha_{aa,t}$, $\alpha_{pa,t}$, and $\alpha_{pa,t}$ are higher in environment one, while the perennial species' fecundity term $\lambda_{p,t}$, survival terms $s_{p,t}$ and $S_{p,t}$, and competitive rates $\alpha_{pp,t}$, $\alpha_{ap,t}$, $\alpha_{pP,t}$, $\alpha_{aP,t}$, and $\alpha_{PP,t}$ are higher in the second environment. All parameter values are provided in Supplementary Tables S1 and S2.

Scenario 2, Water limitation: This scenario aligns with an environment where precipitation varies across years, with wet years being intrinsically favorable for both species. As such, we assume that species have higher demographic rates, including fecundity and survival in the same environment (i.e. in wet years). However, under water stress, competition between species is maximized, as plants compete more strongly for water in dry years. As such, species exert stronger competition in the second "unfavorable" environment (Fig 1D). Translating these model assumptions into parameters, in the simulation between the non-seedbanking annual and the seedbanking annual species, all fecundity and germination rates $\lambda_{a,t}$, $\lambda_{b,t}$, and $g_{b,t}$ are higher in a given environment where all competitive rates $\alpha_{aa,t}$, $\alpha_{ba,t}$, $\alpha_{ab,t}$, and $\alpha_{bb,t}$ are lower. Similarly for the simulation between the non-seedbanking annual and the perennial species, all fecundity and survival rates $\lambda_{a,t}$, $\lambda_{p,t}$, $s_{p,t}$, and $S_{p,t}$ are higher in one environment, and all competitive rates $\alpha_{aa,t}$, $\alpha_{pa,t}$, $\alpha_{pP,t}$, $\alpha_{ap,t}$, $\alpha_{pP,t}$, $\alpha_{aP,t}$, and $\alpha_{PP,t}$ are lower in that environment.

Scenario 3, Light and/or space limitation: Our final scenario considers situations where compe-

288 titution for light or space drives community dynamics. This scenario also aligns with an environ-
 ment where precipitations varies between years and wet years are intrinsically more favorable
 for both species. However, contrasting Scenario 2, in this case, as plants grow larger in wetter
 291 years, they consequently compete more strongly for light due to their larger size. In this scenario,
 both species have higher intrinsic growth rates, including fecundity and survival, in the same en-
 vironment, and species exert stronger competition in this favorable environment (Fig 1E). This
 294 stronger competition may result in lower population growth rates in these years despite benefits
 to vital rates in the absence of competition. For this scenario, all intrinsic vital rates (fecundity,
 germination, and survival) vary as in the light limited scenario, but competitive rates are also
 297 highest in the environment where intrinsic vital rates are high and vice versa.

All simulations and code were executed in R (R Core Team, 2022) using the ‘tidyverse’ and
 300 ‘here’ packages (Müller, 2020; Wickham et al., 2019)

Results

Full partitioning of the storage effect

303 The extended partitioning of $\Delta^{\lambda\alpha}$, commonly referred to as the storage effect, into the true co-
 variance storage effect $\Delta^{(\lambda\alpha)}$ and the remnant interaction term $\Delta^{\lambda\neq\alpha}$ (Ellner et al., 2019) indicated
 that across both coexistence pairs and all scenarios $\Delta^{\lambda\neq\alpha}$ plays a minimal role. This supports the
 306 use of the simpler $\Delta^{\lambda\alpha}$ as a good approximation of the storage effect, which we do for simplicity
 throughout the rest of the manuscript. We show the additional decomposition of $\Delta^{\lambda\alpha}$ into $\Delta^{(\lambda\alpha)}$
 and $\Delta^{\lambda\neq\alpha}$ in Supplementary Figures S1 and S2.

Stage-structured species as invaders

In Scenario 1, different limiting resources, the environment that is intrinsically favorable to each
 of the stage-structured species is unfavorable to their non-seedbanking annual competitor, and

consequently both Δ^0 and their full low-density growth rates (ldgr) are highest at a high frequency of this intrinsically favorable environment (Fig 2A and B; green and black lines). Ldgr in this scenario can be reasonably approximated by averaged Δ^0 , although Δ^λ does increase ldgr for both stage-structured species and consequently expands the region of coexistence. Δ^α and $\Delta^{\lambda\alpha}$ play minimal roles for both stage-structured species.

In Scenario 2, water-limitation and Scenario 3, light-limitation, neither ldgr nor Δ^0 of the stage-structured species are maximized at a high frequency of the environment that is intrinsically favorable to them, because this environment is also favorable to their non-seedbanking annual competitor. In these scenarios, fluctuation-dependent mechanisms are strong contributors to ldgr of both stage-structured species (Figure 2C - F). In both Scenario 2–water-limitation and Scenario 3–light-limitation, Δ^λ is the strongest of these mechanisms, and has a larger impact than the variation-independent Δ^0 across most of the environmental frequencies. As such, the true optimal environments where ldgr is maximized is $\leq 50\%$ the optimal environment for vital rates. For the perennial species in particular, Δ^λ often outweighs Δ^0 , to the extent that in Scenario 2 the full ldgr is actually highest in roughly 50:50 ratios of the intrinsically favorable and intrinsically unfavorable environment conditions despite Δ^0 being lowest in this region (Figure 2C). For the seedbanking annual species, full ldgr is lowest at a high frequency of its intrinsically favorable environment (Figure 2D), in which competition is also highest.

Some coexistence patterns differ between the perennial and seedbanking annual species. In both Scenario 2–water-limitation and Scenario 3–light-limitation, averaged fitness Δ^0 varies more across environmental ratios for the seedbanking annual (Fig 2 D and F) than for the perennial (Fig 2 C and E). The difference between Scenario 2 and Scenario 3 is that the covariance of λ and α switches from negative in Scenario 2–water limitation (lower competition in intrinsically favorable years) to positive in Scenario 3–light-limitation (higher competition in intrinsically favorable years). This shift consequently flips the impact of the storage effect $\Delta^{\lambda\alpha}$ from positive to negative, as favorable environments now also have stronger competition in Scenario 3 (Fig 2 D and F). The change in the direction of the storage effect impacts both stage-structured species,

but is particularly important for the perennial species, as it changes the perennial ldgr pattern from having a clear optimum environmental frequency (Fig 2C) to a nearly flat relationship with frequency of environmental conditions (Fig 2E).

Stage-structured species as residents

In mixed communities with stage-structured species as residents (rather than as invaders, as in Figure 2), fluctuation-dependent mechanisms are minimally important for the ldgr of the non-seedbanking annual species in Scenario 1, different limiting resources (opposite environments are favorable for the interacting species; Figure 3 A and B). Rather, coexistence dynamics are driven primarily by fluctuation-independent mechanisms, Δ^0 . In contrast, fluctuation-dependent mechanisms are key drivers of ldgr for the non-seedbanking annual invader of stage-structured resident species in both Scenario 2, water-limitation and Scenario 3, light-limitation, when the same environment is intrinsically favorable for both interacting species (Figure 3 C - F). In Scenario 2, water-limitation, all three fluctuation-dependent mechanisms Δ^λ , Δ^α and $\Delta^{\lambda\alpha}$ are negative for the non-seedbanking annual invader, regardless of the environmental ratio (Figure 3 C and D). These fluctuation-dependent mechanisms are particularly important when the perennial species is the resident, resulting in a ldgr that is negative for all but $> 75\%$ intrinsically favorable environments even though the averaged Δ^0 is positive across the gradient of environmental ratios. The strength of these fluctuation-dependent mechanisms results in the lowest full ldgr in the environmental ratio where Δ^0 is highest (Figure 3 C). Although the fluctuation-dependent mechanisms in Scenario 2, water limitation, are also negative when the seedbanking annual is the resident, Δ^0 is a stronger overall driver of the patterns of the full ldgr rate, contrasting with the perennial case.

The difference between Scenario 2, water-limitation (weaker competition in the favorable environment) and Scenario 3, light-limitation (stronger competition in the favorable environment) is much more pronounced with the perennial resident than the seedbanking annual resident. When the perennial is resident, the non-seedbanking annual can only persist at a high frequency of an intrinsically favorable environment in Scenario 2, water-limitation (Figure 3 C), but has a

positive ldgr across all environmental frequencies in Scenario 3, light-limitation (Figure 3 E). In contrast, although the storage effect with the seedbanking annual resident also switches direction between these two scenarios, it has a smaller impact, while average fitness Δ^0 is a more dominant driver of the overall lgr (Figure 3 D and F) regardless of scenario.

Discussion

Simulation-based approaches to modern coexistence theory advance the integration of theory with empirical studies by expanding the scope and complexity of models and systems where coexistence theory can be applied. This simultaneously expands our understanding of basic community ecology while increasing our ability to apply coexistence concepts across systems (Letten et al., 2018; Shoemaker et al., 2020) and even to management practice (Hallett et al., 2023). However, the majority of coexistence theory models have made simplifying assumptions based around interactions between annual species, with a smaller body of work on all-perennial communities (e.g., Adler et al. 2006; Chu and Adler 2015). Here we extended modern coexistence theory both conceptually and analytically to reflect mixed annual-perennial communities. We demonstrate that the same fluctuation-dependent coexistence mechanisms that structure seedbanking annual communities can support perennial species in mixed communities. Notably, however, the difference in how these life forms “store” during unfavorable times can leads to differences – with perennials continuing to exert competitive effects but annuals dormant in the seedbank – in their optimal level of environmental fluctuations and role as resident species. For example, when competing against a non-seedbanking annual that intrinsically favored the same environment, the ldgr of seedbanking annuals was highest in a high frequency of their non-optimal environment due to competitive release, whereas the ldgr of perennial species was maximized at intermediate frequencies of the two environments due to the benefit from relative non-linearity. Our study highlights the importance of environmental fluctuations for coexistence of mixed communities and contrasts scenarios when inferences from annual systems can or can-

not be applied in mixed communities.

Under a scenario in which the focal stage-structured species and non-seedbanking annual competitor intrinsically favor opposite environments, the effect of environmental variability on perennial and seedbanking annual species is much the same: the ldgr of both life forms increases linearly with the frequency of their favorable environment, owing largely to average fitness differences and more minorly to relative nonlinearity in seed production. This scenario can be thought of as essentially a “null” scenario in which fluctuation-dependent coexistence mechanisms are of minimal importance. Instead, the ldgr of either individual species increases with the frequency of its optimal environment, and coexistence between species depends solely on each species experiencing its optimal environment with sufficient frequency. Thus, when a focal species and its competitor are expected to have different directional responses to the environment, patterns observed in annual plant communities are likely to be predictive of dynamics in mixed perennial-annual communities. This pattern of coexistence might arise from species with different responses to nutrient composition, similar to an R^* resource competition framework (Tilman, 1982), strong niche differentiation (Carscadden et al., 2020; Germain et al., 2021), or different optimal temperature conditions (Jiang and Morin, 2007).

Fluctuation-dependent mechanisms had a much stronger impact on the ldgr of both the focal perennial and seedbanking annual species when their non-seedbanking competitor intrinsically favor the same environment, with many generalities between the perennial and seedbanking annual. In this case, a negative covariance between density-independent growth and competitive strength (corresponding to the water-limited scenario) resulted in a positive storage effect for both stage-structured life forms, whereas a positive covariance between density-independent growth and competitive strength (corresponding to the light- or space-limited scenario) resulted in a negative storage effect for both perennial and seedbanking annual species. Analyzing empirically-derived parameters for these models could therefore provide insight into the balance of limiting factors for species interactions in a given community: a positive storage effect might indicate a water-limited system, while a negative storage effect would point to a light- or space-limited

system. Indeed, some of the strongest evidence of a positive storage effect in annual plants come from deserts, where water limitation is likely the strongest driver (Angert et al., 2009; Holt and Chesson, 2014; Sears and Chesson, 2007), whereas in semi-arid grasslands, where space- and light-limitation may intensify competition in wet years, the storage effect has been observed to play a weaker, and at times negative, role (Aoyama et al., 2022; Hallett et al., 2019). Similarly, the strength and direction of fluctuation-dependent coexistence mechanisms in response to the frequency of favorable environmental conditions was largely the same among perennial and seedbanking annuals. Relative nonlinearity positively contributed to ldgr under all scenarios and was strongest at more even ratios of the environmental conditions, which correspond to higher environmental variability. These patterns are consistent across mixed communities with different stage-structured life history patterns.

Pronounced differences emerge between perennial and seedbanking annual species, however, in the degree to which their ldgr was driven by fluctuation-dependent coexistence mechanisms in relation to the frequency of favorable environmental conditions, especially when their non-seedbanking competitor intrinsically favor the same environment (i.e., under water limitation or light/space limitation). As an invader, the perennial experienced less of a difference in its ldgr under differing frequencies of favorable versus unfavorable environments compared to the seedbanking annual. This reflects a common pattern among perennial species in which population viability is largely a function of adult growth and survival rather than seed production or seedling performance (Larios and Hallett, 2022; Zucaratto et al., 2021), whereas population viability of a seedbanking annual requires at least some periods of high seed production – either due to direct demographic responses or competitive release – which should be reflected in ldgr (Stump and Vasseur, 2023; Van Dyke et al., 2022). Because the average ldgr between environmental conditions varied little for the perennial, the response of its overall ldgr to the frequency of favorable environmental conditions largely tracked fluctuation-dependent coexistence mechanisms, resulting in a hump-shaped relationship under water limitation driven by relative nonlinearity, and a flat relationship under light/space limitation when the effects of relative nonlinearity and the

444 storage effect canceled out. In contrast, as an invader, the ldgr of the seedbanking annual was
driven largely its response to average environmental conditions, consistently declining with the
increasing frequency of the environment favorable for its density-independent growth as the
447 negative effects of high competition overwhelmed the intrinsic benefits of this environment. The
comparison underscores the importance of competition for mediating species responses' to fluc-
tuations, and the need to jointly consider species interactions and environmental variability for
450 predicting perennial persistence and coexistence (Lyu and Alexander, 2023; Paniw et al., 2023).

Differences in how species “store” across unfavorable environments also led to pronounced
differences in how perennial and seedbanking annuals altered the ldgr dynamics of their non-
453 seedbanking annual competitor. Because the perennial species' key storage buffering stage is
as an adult, it exerts competitive effects in this stage across both favorable and non-favorable
environments. This decreases invasion growth rates for the non-seedbanking annual due to the
456 destabilizing role of the storage effect on the invader. In contrast, the buffering storage stage for
seedbanking annuals is as dormant seeds, during which it does not interact competitively with
the invading species. This difference has strong impacts on the strength of fluctuation-dependent
459 mechanisms, including the storage effect (Stump and Vasseur, 2023), in mixed communities.
The combination of the storage effect and relative non-linearity are the dominant drivers of
ldgr and competitive exclusion of the non-seedbanking annual interacting with the perennial
462 resident, while average fitness was the dominant driver of ldgr of the non-seedbanking annual
with the seedbanking annual resident. Again these fluctuation-dependent mechanisms were only
important when both interacting species favored the same environment, and especially important
465 when competition intensified under intrinsically favorable conditions (water-limited scenario).

Natural ecological systems overwhelmingly include mixed communities with coexisting species
of diverse life history strategies and stage structure. Even grassland systems, often used as model
468 ecological communities for developing and testing theory, are predominantly mixed annual-
perennial systems, while annual-only systems are actually fairly rare anomalies (Cleland et al.,
2013). By providing an analytical model that can be applied to more diverse empirical systems,

our approach opens the door to a broader understanding of coexistence and community dynamics in ecological communities, ideally facilitating future empirical tests in mixed communities. Further, it examines which assumptions from annual communities may or may not extend to mixed communities. For simplicity we limited our stage-structured species to two life stages, but more detailed population dynamics using integral projection models or seedbanking perennial species would further improve our understanding of mixed community dynamics (Dahlgren and Ehrlén, 2009; Doak et al., 2021). Lastly, a key goal for community ecology is scaling up from pairwise coexistence models to understanding species interactions in diverse communities, and this could be especially important in multi-species communities with diverse life history strategies (Chamberlain et al., 2014; Levine et al., 2017; Weiss-Lehman et al., 2022).

Increasing, modern coexistence theory is being tested empirically and even applied for management, especially as the importance of variation and species interactions is moving to the foreground of community ecology (Brudvig et al., 2017; Chase, 2003; Cleland et al., 2013; Werner et al., 2020). Current applications include predicting how species will respond to climate change, including changing rainfall conditions (Hallett et al., 2019; Paniw et al., 2023; Van Dyke et al., 2022) or climate-driven range shifts (Usinowicz and Levine, 2021; Yang et al., 2022), with a framework that considers changing frequencies of different conditions and extremes rather than oversimplifications of average changes. Applications of modern coexistence theory to restoration management have also been proposed, especially using coexistence dynamics to predict the success of actions intended to increase populations of desirable species or reduce populations of invasive species (Aoyama et al., 2022; Bowler et al., 2022; Hallett et al., 2023; Yu and Li, 2020). Because mixed perennial-annual communities are nearly ubiquitous across terrestrial systems, an expanded modern coexistence theory framework for use in mixed systems is vital to our ability to apply this powerful tool in most ecological systems.

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Figure Legends

Figure 1: Conceptual figure of population growth models with species interactions for (A) interactions between non-seedbanking annual and seedbanking annual species (B) non-seedbanking annual and perennial species. (C-E) Species' intrinsic growth rates and competitive strengths differ between two environments for our three different environmental scenarios. (C) Each species is favored by a different environment, and each exerts stronger competition in its favored environment (ex: different limiting resources). (D) The same environment is favorable for both species' vital rates, and both species exert stronger competition in the intrinsically unfavorable environment (ex: competition for water). (E) The same environment is favorable for both species' intrinsic growth rates, and both species exert stronger competition in this favorable environment (ex: competition for light or space). (F) Partitioning of low density growth rate into its mechanistic contributions: Δ^0 is the difference in average growth rates under a constant environment, Δ^λ quantifies the direct effect of environmental variation on demographic rates, Δ^α quantifies the direct effect of environmental variation on competition, and $\Delta^{\lambda\alpha}$ quantifies the interaction. $\Delta^{\lambda\alpha}$ can be further decomposed into a combination of the storage effect, $\Delta^{(\lambda\alpha)}$, and the remaining interaction effect with covariance removed, $\Delta^{\lambda \neq \alpha}$.

Figure 2: Comparison of low density growth rates and coexistence mechanisms across the three environmental scenarios (rows) for the perennial invading into a non-seedbanking annual as the resident (first column) and seedbanking annual invading into a non-seedbanking annual (second column). The x-axis denotes different environmental time series, ranging from fully unfavorable for the invader to a fully favorable time series, with 50:50 an even mix through time of the two environmental conditions. Low density growth rate (black) is partitioned into its components: fluctuation independent averaged growth rate (green; Δ^0), relative nonlinearity in growth (blue; Δ^λ), relative nonlinearity in competition (yellow; Δ^α), and their interaction (purple; $\Delta^{\lambda\alpha}$). Shaded regions denote one standard deviation.

Figure 3: Comparison of low density growth rates and coexistence mechanisms across the three environmental scenarios (rows) for the non-seedbanking annual invading into the perennial as the resident (first column) and into the seedbanking annual as the resident species (second column). As in Figure 2, the x-axis denotes different environmental time series, ranging from fully unfavorable for the invader to a fully favorable time series. Low density growth rate (black) is partitioned into its components: fluctuation independent averaged growth rate (green; Δ^0), relative nonlinearity in growth (blue; Δ^λ), relative nonlinearity in competition (yellow; Δ^α), and their interaction (purple; $\Delta^{\lambda\alpha}$). Shaded regions denote one standard deviation.