Functional tradeoffs determine species coexistence via the storage effect

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How biological diversity is generated and maintained is a fundamental question in ecology. Ecologists have delineated many mechanisms that can, in principle, favor species coexistence and hence maintain biodiversity. Most such coexistence mechanisms require or imply tradeoffs between different aspects of species performance. However, it remains unknown whether simple functional tradeoffs underlie coexistence mechanisms in diverse natural systems. We show that functional tradeoffs explain species differences in long-term population dynamics that are associated with recovery from low density (and hence coexistence) for a community of winter annual plants in the Sonoran Desert. We develop a new general framework for quantifying the magnitude of coexistence via the storage effect and use this framework to assess the strength of the storage effect in the winter annual community. We then combine a 25-year record of vital rates with morphological and physiological measurements to identify functional differences between species in the growth and reproductive phase of the life cycle that promote storage-effect coexistence. Separation of species along a tradeoff between growth capacity and low-resource tolerance corresponds to differences in demographic responses to environmental variation across years. Growing season precipitation is one critical environmental variable underlying the demographic decoupling of species. These results demonstrate how partially decoupled population dynamics that promote local biodiversity are associated with physiological differences in resource uptake and allocation between species. These results for a relatively simple system demonstrate how long-term community dynamics relate to functional biology, a linkage scientists have long sought for more complex systems.

biodiversity | coexistence mechanism | functional trait | population dynamics | specific leaf area

How competing species stably coexist is a long-standing ecological problem. All niche-based mechanisms for stable coexistence rely on ecological differences that enable each species to recover when perturbed to low density and thus remain in the community. Some of these coexistence mechanisms, such as differential exploitation of multiple limiting resources (1, 2) and frequency-dependent predation (3), operate independently of fluctuations in the environment. Other stable coexistence mechanisms depend critically upon environmental fluctuations that allow species to recover from low density (4). These include competition/colonization tradeoffs in a disturbance matrix (5, 6), relative nonlinearity of competition (7) and the storage effect (8, 9). The storage effect combines species-specific responses to the environment and population-dynamic buffering by persistent life history stages in a way that results in a positive average low-density growth rate for each species. It is perhaps the dominant fluctuation-dependent mechanism for organisms in variable environments. Its role has been explored for diverse groups ranging from freshwater zooplankton (10) and coral reef fishes (8) to desert annuals (11), prairie grasses (12) and tropical trees (13), but in no case is the mechanism underlying species-specific responses to the environment well-understood. Specifically, temporal environmental variation increases coexistence through the storage effect when (*i*) demographic decoupling of species arises from partially uncorrelated responses to environmental variation, (*ii*) the strength of competition covaries with environmental conditions, and (*iii*) certain life history traits, such as seed banks or long-lived adults, limit the impact of competition in unfavorable environments (4, 9). Here, we address the critical challenges of identifying the functional differences between species that create demographic decoupling and quantifying their relationship to species coexistence (14).

The winter annual species of the Sonoran Desert have played an important role in the development and testing of general concepts about fluctuation-dependent community dynamics (11, 15) because they form a mature, persistent community where unpredictable weather creates substantial demographic variability. Desert annual germination is controlled by temperature and rainfall, and winter and summer rains in the Sonoran Desert give rise to distinct winter and summer annual plant communities. Annuals comprise up to 50% of the desert flora and have been the subject of classic investigations on physiology and population dynamics (16, 17). Winter annuals complete their life cycles within a few weeks to months. Their short life cycles, small size and sessile habit permit the monitoring of many individuals throughout their entire life cycle and the observation of multiple generations during the course of a single long-term project. These qualities enable quantitative estimates of the probability distributions that are critical to fluctuation-dependent theories. Desert annuals meet a key requirement for storage-effect coexistence: long-lived seed banks buffer populations during unfavorable periods (18). Also, by definition, years that favor high germination directly result in greater density, creating positive covariance between an environmental parameter and competition. A similar environment-competition covariance arises from varying environmental factors affecting seedling survival and individual growth, because higher survival and larger survivors increase demand for resources (19). Although these effects reduce the ability of a high density species to take advantage of favorable environment conditions, it does not alter our ability to measure the relative responses of different species to the environmental conditions.

Coexistence is promoted if a set of species is buffered by persistent seed banks and if species' environment-competition covariances decline when their densities decline. These effects create low-density advantages, and occur when there is sufficient demographic decoupling between species driven by differences in their responses to temporally varying physical environmental conditions (15, 19). In desert annuals, such demographic responses can be suitably divided into germination and fecundity. Decoupling through germination is a well-known and well-studied scenario by which low-density advantages are created (9, 15, 20). Decoupling

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through reproduction, which is the focus of this article, reflects the combined effects of survival and growth (19), and provides strong low-density advantages, which we show here (*SI Appendix*). The decoupling of reproductive success between species that promotes species coexistence can be measured as the statistical interaction between species and time for per germinant fecundity.

In this article, we present a general framework for quantifying the magnitude of the storage effect, assess the strength of the storage effect in a community of Sonoran Desert winter annuals, and identify functional differences between species in the growth and reproductive phase of the life cycle that promote storage-effect coexistence. We have examined interspecific variation in traits associated with resource uptake and resource allocation for 9 coexisting Sonoran Desert winter annuals to test the hypothesis that fundamental tradeoffs in plant function create the differential demographic responses to environmental variation that help maintain diverse species assemblages in plant communities. Specifically, we look for a relationship between functional trait variation and the species-by-time interaction for reproduction that contributes quantitatively to recovery from low density. Elucidating such functional links in annual plants should provide insights relevant to less tractable systems.

Results and Discussion

Using a dataset collected annually from 1982 to 2007 from 72 permanently marked quadrats, we obtained estimates of germination, survival and fecundity, and used these data to estimate variance components by standard ANOVA methods. Sonoran Desert winter annual species exhibit striking demographic fluctuations (11) and respond in partially dissimilar ways to yearly variation, as evidenced by species-by-year interactions for ln-transformed per capita germination ($F_{105,91} = 6.44, P < 0.0001$) and per germinant fecundity ($F_{165,2926} = 7.99, P < 0.0001$) (Table S1). For our system, the low-density advantage due to germination variation alone increases $\bar{r}$ by $\approx$0.052, while that due to reproductive variation alone adds 0.025 to $\bar{r}$, where $\bar{r}$ is the species average recovery rate from low density (the low-density long-term per capita population growth rate) (Table S2 and *SI Appendix*). An additional increase to $\bar{r}$ of 0.027 comes from the covariance of germination fraction and reproductive variation, giving a total storage effect of 0.103 (Table S2). For a system as large as this one (millions of individuals of most species at one field station), recovery rates need only be positive for indefinite coexistence (8, 9). The observed storage effect is a substantial population growth rate for a species bouncing back from low density in competition with other species (equivalent to a doubling time of 7 years).

To understand how differences in functional traits create population dynamic decoupling, we examined interspecific variation in traits related to growth, allocation and low-resource tolerance and related these differences to the species-by-year interaction for per germinant fecundity. A fundamental tradeoff thought to be important in plants is that between the ability to photosynthesize and grow rapidly versus the ability to withstand the stresses inherent in low resource environments (21, 22). Such a tradeoff has been described across life forms, but we find the tradeoff within one functional guild (Fig. 1) (23). Sonoran Desert winter annuals are arrayed along a tradeoff between relative growth rate (RGR) and a measure of intrinsic water-use efficiency (WUE), carbon isotope discrimination [Δ, where lower Δ indicate higher intrinsic WUE (24)] (Fig. 1). Species with high RGR exhibit low WUE, whereas species with high WUE have low RGR. Our prior work has identified the key morphological and physiological traits that underlie growth capacity and low-water tolerance in these species (23, 25). Species that display high growth capacity allocate a large fraction of biomass to photosynthetic surfaces and have the ability to rapidly deploy large leaf area displays to maximize growth after infrequent,

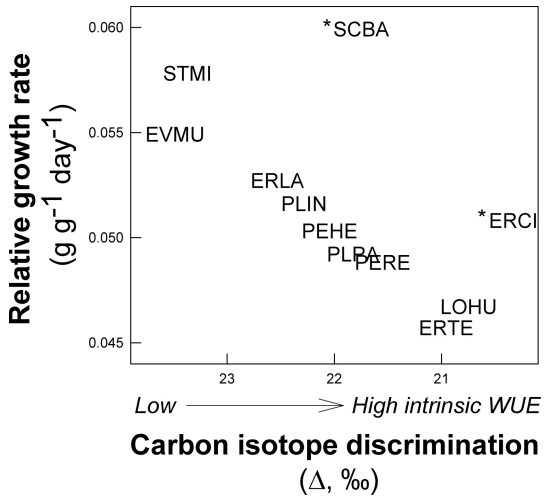

Fig. 1. Interspecific tradeoff between growth capacity (relative growth rate, RGR, in $g \cdot g^{-1} \cdot day^{-1}$) and low-resource tolerance (intrinsic water-use efficiency, assayed by leaf carbon isotope discrimination, Δ, ‰). Species abbreviations are the first two letters of the genus and specific epithet given in *Materials and Methods*. Asterisks (*) denote 2 naturalized species.

large rainfall events (23). Conversely, species that display high intrinsic WUE invest a large fraction of leaf nitrogen in the photosynthetic processes that become limiting at low temperatures characteristic of postrainfall periods, which optimizes carbon assimilation for the short windows of time after small but relatively frequent rain events (25). To capture this complexity, we conducted a principal components analysis of these traits that reflect physiological and morphological capacities underlying the growth/low-resource tolerance tradeoff: specific leaf area (SLA), leaf mass ratio (LMR), relative growth rate plasticity, the ratio of maximum electron transport to maximum carboxylation velocity (J_{max}:V_{Cmax}), and leaf nitrogen content (N_{leaf}). Scores on the first principal component contrast species with high leaf mass allocation, leaf N, and electron transport capacity (which optimizes carbon assimilation at low temperatures after small rainfall events) versus species that attain high growth via high leaf area investment and morphological plasticity after large rainfall events (Table 1). Species' pairwise differences in PC I scores quantify composite differences in the key physiological traits that underlie the growth rate/low-resource tolerance tradeoff.

To calculate species' differences in response to year, we first decomposed the species-by-year interaction for per germinant fecundity into a residual effect for each species in each year after removing main effects and sampling error (Fig. 2). We then squared species' pairwise differences in residual interaction terms. The average over pairs of species and time of these squared pairwise differences estimates the species-by-year interaction component of variance that is used to calculate the magnitude of the storage effect due to fecundity (*SI Appendix*). The average squared differences between species in these interaction effects were placed in a 9×9 matrix that describes species' pairwise contributions to the species-by-year interaction term, and hence, the magnitude of their contributions to the demographic differences that promote coexistence (Table S3). Species that respond similarly to yearly variation will tend to have low differences, whereas species that respond dissimilarly to yearly variation will tend to have high differences. Using a matrix correlation approach, we find that the matrix of species differences in PC I scores (Table S4) is highly correlated with the matrix of contributions to the species-by-year interaction (Mantel test, $P = 0.0003$) (Fig. 3*A*). The

Table 1. Trait loadings, species scores, and percent variation explained by the first principal component of variation (PC I) in functional traits

PC I results	Species or trait	Analysis 1	Analysis 2
Trait loading	LMR	−0.8293	
	J_{max}:V_{Cmax}	−0.4611	
	N_{leaf}	−0.5927	
	SLA	0.9128	
	RGR plasticity	0.7855	
	Δ		0.9914
	RGR		0.9914
Species score	*ERCI*	−0.7781	−1.3221
	ERLA	1.2518	0.6663
	ERTE	−1.1007	−1.7816
	EVMU	3.2855	1.7764
	LOHU	−0.7294	−1.7539
	PEHE	−0.6152	−0.1351
	PERE	−2.1561	−0.7760
	PLIN	−0.7775	0.2810
	PLPA	−0.4514	−0.4976
	SCBA	0.8267	1.3805
	STMI	1.2930	2.2205
Variation explained		54%	98%

Analysis 1: leaf mass ratio (LMR), maximum electron transport capacity (J_{max}:V_{Cmax}), leaf nitrogen content (N_{leaf}), specific leaf area (SLA), and growth plasticity (RGR plasticity). Analysis 2: relative growth rate (RGR) and carbon isotope discrimination (Δ; inversely related to intrinsic water-use efficiency).

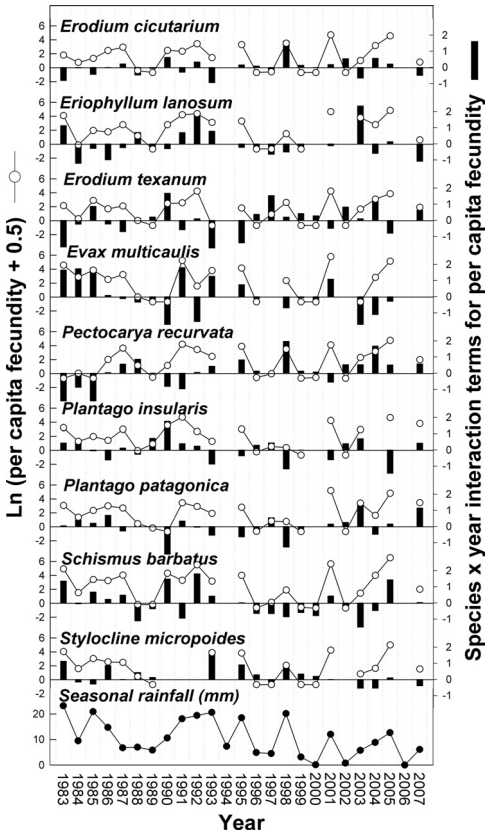

Fig. 2. Annual per germinant fecundity (survivorship to reproduction, *l*, times fecundity, *b*) for each species (left axis, lines) and decomposition of the species-by-year interaction for per germinant fecundity into effects for each species and year after subtracting species and year main effects and sampling error (right axes, black bars). If the species-by-year interaction effects are positive, then *lb* was greater than expected based on the main effects of species and year alone. (*Lower*) Interannual variation in growing season precipitation (total precipitation from the first germination-inducing rain until the final reproductive census each year).

relationship remains highly significant using a partial Mantel test with a third matrix of phylogenetic distances (Table S5). This finding provides a mechanistic explanation of how functional traits underlie species differences in population dynamic responses to the environment of different years. To see if this relationship can be captured with simpler integrative measures, we recalculated the matrix correlations using the PC I score based on the emergent growth rate/low-resource tolerance tradeoff alone. The matrix of species differences along the RGR-Δ tradeoff (Table S4) is also significantly related to the matrix of species contributions to the species-by-year interaction, but with a lower P value (Mantel test, $P = 0.0410$) (Fig. 3*B*). Thus, while a simple functional tradeoff is involved in the demographic decoupling that contributes to coexistence, explicit recognition of variation in the underlying parameters suggests a more intricate relationship between physiology and coexistence.

Temporal demographic decoupling captured by the species-by-year interaction reflects differences in demographic response to environmental variation. We investigated the relationship between demography, traits, and climate variables to determine how the environments of different years, operating through these functional traits, result in differential performance. Because precipitation controls the rate and timing of most biological processes in arid ecosystems (26), we hypothesized that differential response to precipitation is a major contributor to the species-by-year interaction. Species differ strongly in their demographic responses to precipitation (species by precipitation, $F_{8,3104} = 11.77, P < 0.0001$). We described each species' demographic sensitivity to precipitation as the slope of the relationship between per germinant fecundity and growing season precipitation. The matrix of species squared differences in demographic sensitivity to precipitation (Table S3) correlates with the matrix of contributions to the species-by-year interaction (Mantel test, $P = 0.0075$). Differences in demographic sensitivity to other climate parameters, such as growing season length and temperature, are not significantly related to the pairwise contributions to the species-by-year interaction (Mantel tests: season length, $P = 0.30$; average maximum temperature, $P = 0.50$; average minimum temperature, $P = 0.72$). Furthermore, the matrices of species differences in functional traits are significantly related to the matrix of differential demographic sensitivity to precipitation (Mantel tests: 5-trait matrix, $P = 0.0068$; RGR-Δ matrix, $P = 0.0453$). Thus, tradeoffs in key physiological processes that result in different utilization of soil moisture explain demographic decoupling that is driven by inter-annual variation in precipitation.

We have shown that the same fundamental tradeoff between growth capacity and low-resource tolerance that separates life forms (21, 22) is found within what is commonly considered to be 1 plant functional type. The degree of separation between species on this tradeoff axis is quantitatively related to the magnitude of their differential demographic response to environmental variation between years, specifically variation in the amount of growing season precipitation. Incorporation of lower-level functional traits that describe resource uptake and allocation behavior produces a more exact description of how physiological differences between species explain the temporal population dynamics that promote local biodiversity via the storage effect. These tests have relied on an extension of storage-effect theory to consider different degrees of decoupling between different pairs of species (*SI Appendix*). Although not required in theory for the storage effect (9), it stands to reason that more physiologically similar species are demographically more similar too. Recognition of such differences leads to the approaches for understanding the factors driving demographic

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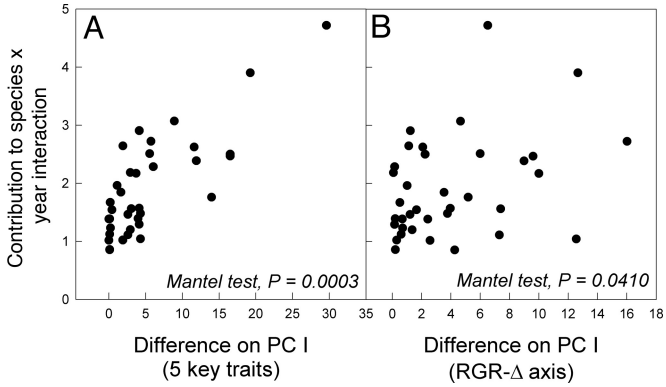

Fig. 3. Species differences in response to yearly variation are correlated with differences in position along the first principal component of variation in 5 key functional traits that underlie a growth capacity/low-resource tolerance tradeoff (leaf mass ratio, maximum electron transport capacity, specific leaf area, relative growth plasticity and leaf nitrogen content) (*A*) and differences in position along the first principal component constructed using relative growth rate and intrinsic water-use efficiency alone (*B*). Each point represents the pairwise squared difference between 2 species. Significance was tested with Mantel permutation tests to account for non-independence of data points.

decoupling that we have demonstrated here. The results from this investigation of short-lived plants in extreme environments should provide an important reference point for our emerging understanding of more complex communities.

Materials and Methods

From 1982 to 2007, permanent plots at the University of Arizona Desert Laboratory (Tucson, AZ) were censused after each rainfall to document germination, survivorship to reproduction (*l*), and fecundity (*b*) of all winter annual species (18). Species with at least 5 individuals in each of at least 15 years (76% of all seedlings in the dataset) were selected for analysis of *lb*: *Pectocarya recurvata* (Boraginaceae), *Erodium cicutarium*—naturalized, *Erodium texanum* (Geraniaceae), *Eriophyllum lanosum*, *Evax multicaulis*, *Stylocline micropoides* (Asteraceae), *Plantago insularis*, *Plantago patagonica* (Plantaginaceae) and *Schismus barbatus*—naturalized (Poaceae).

During 2004–2005, we measured functional traits of these species plus *Lotus humistratus* (Fabaceae) and *Pectocarya heterocarpa*, which were abundant that year. We determined relative growth rate (RGR), specific leaf area (SLA) and leaf mass ratio (LMR) by harvesting up to 30 plants per species biweekly throughout the season (see ref. 24). We calculated V_{Cmax} (maximum carboxylation rate by Rubisco) and J_{max} (maximum light-saturated electron transport rate) from assimilation versus internal CO_2 concentration curves on fully expanded leaves of 3 to 5 individuals per species (see ref. 26). Leaf nitrogen (N_{leaf}) and carbon isotope composition were analyzed at the University of Arizona Geosciences Stable Isotope Facility. Carbon isotope ratios were converted to discrimination values (Δ) (27).

We used ANOVA to assess the effects of species, year (or ln-seasonal precipitation) and their interaction on ln-transformed plot-level per germinant fecundity (*lb* + 0.5), weighted by the number of seedlings per species per plot (PROC GLM, SAS 9.1; SAS Institute). Significance of effects was tested with Type III sums of squares. We added 0.5 to *lb* because ln(0) is undefined, and *lb* occasionally equalled 0 if no seedlings of a given species germinated on a particular plot or if few seedlings of a given species germinated but all died before reproduction. Results were qualitatively identical when different constants were added to per germinant fecundity (e.g., *lb* + 0.17 or *lb* + 1). Results also were qualitatively identical when untransformed data were analyzed with generalized linear models (gamma distribution, log link function; PROC GLIMMIX). We decomposed the species-by-year interaction into an interaction effect for each species in each year based on the following equation: Interaction(S_i, Y_j) = LS(S_i, Y_j) − LS(S_i) − LS(Y_j) + LS(grand mean), where LS denotes the least-squares mean estimate for a particular species, S_i, year, Y_j, or S_i, Y_j combination. We used the ''LSMEANS'' statement of PROC GLM to obtain least-squares means for each S_i, Y_j and S_i, Y_j combination. The interaction(S_i, Y_j), when squared and summed over years, divided by the degrees of freedom, and corrected for sampling error, gives us the species x year interaction component of variance ($\sigma^2_{V,t\times s}$) for log per germinant fecundity, ln(*lb*), used to calculate the magnitude of the storage effect (Tables S1 and S2 and *SI Appendix*).

To see how this population dynamic interaction relates to species functional biology, we first expressed it as a species difference matrix. For each pair of species, we calculated the average of squared differences in their interaction effects by summing the squares of their differences in each year (excluding any years in which one of the species remained dormant) and then dividing by the number of years in which both species were observed in the vegetative phase (n = 19–23 years). These differences between species were placed in a 9 × 9 matrix describing species' pairwise contributions to the species-by-year interaction term (Table S3, upper diagonal). Species differences in demographic sensitivity to climate variables were estimated as squared differences in slopes of individual regressions of ln(*lb* + 0.5) versus growing season precipitation (Table S3, lower diagonal), season length, average maximum temperature or average minimum temperature. Daily precipitation was recorded at the University of Arizona Desert Laboratory. Daily temperature data were obtained from the University of Arizona weather station ≈5 km from the Desert Laboratory (National Climatic Data Center, National Oceanic & Atmospheric Administration, Asheville, NC)

To summarize interspecific variation in functional traits, we conducted principal component analysis on trait correlation matrices using SAS INSIGHT. The first analysis described species differences in 5 key traits that underlie the growth capacity/low-resource tolerance tradeoff: SLA, LMR, RGR plasticity, J_{max}:V_{Cmax}, and N_{leaf}. The second analysis described species differences in position along the emergent tradeoff between RGR and Δ. We ran the principal component analysis using data from all native species and then manually calculated the 2 naturalized species' scores on the first principal component (PC I) by using the standardized regression coefficients relating each trait to PC I. However, our results do not change when all species are included in the principal component analysis. For each analysis, squared differences between species in PC I scores were placed in a 9 × 9 matrix of functional trait differences (Table S4).

Associations between trait and demographic difference matrices were examined using Mantel tests (28) [program supplied to D.L.V. by E. J. Dietz (Department of Mathematics and Computer Science, Meredith College, Raleigh, NC) and D. E. Cowley (Department of Fish, Wildlife and Conseration Ecology, New Mexico State University, Las Cruses, NM)]. Correlations of corresponding cells of each pair of matrices were calculated with Mantel's *Z*. Permutations preserving the dependencies between matrix elements were performed and the *Z* statistic was recalculated 4,000 times, generating a null distribution against which the observed statistic was tested.

We calculated phylogenetic distance matrices to assess the effects of phylogenetic history on our results. To estimate phylogenetic distances, we first used the online tool Phylomatic (29) to create a hypothesis of the relationships among species based on the conservative seed plant tree available at the Angiosperm Phylogeny Website (30). We created 2 trees, one with equal branch lengths and one with pseudo branch lengths based on ages given by Wikstrom et al. (2001) (31). We calculated matrices of pairwise phylogenetic distances using the *phydist* function in Phylocom (32). We then conducted partial Mantel tests to assess the relationship between the residuals of the demographic and trait difference matrices after removing phylogenetic distance from each. Partial Mantel tests were conducted, using the *R* platform (compilation 2.6.2) and using the package *vegan*. With all analyses, the results from partial Mantel tests controlling for phylogenetic distance were qualitatively identical to results from Mantel tests without phylogenetic matrices (Table S5).

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Supporting Information Text

Derivation of the community average storage effect. Here we present the theory for the storage effect given in the text. We derive formulae for the community average storage effect, which indicates how strongly the storage effect promotes coexistence in terms of how much it increases long-term low-density growth rates, on average(1). This approach is appropriate for quantifying coexistence because coexistence is a community-level property. In the next section (*Quantification of the magnitude of the storage effect*), these results are applied to the data from this system. Readers interested primarily in the application can go immediately to that section, which is self-contained.

The model we use is the seed bank model of Chesson et al.(2) applied in a temporal context, modified for lottery competition. Key quantities in that model are the fraction of seeds of species j germinating in year t, $G_j(t)$, the survival and the growth of the germinating seedlings (vigor), $V_j(t)$, the yield of new seeds per unit plant biomass, Y_j, the competition, $C'(t)$, experienced by the growing plants, and finally, the survival, s_j, of seeds that remain dormant in the seed bank. The model can now be written

$$N_j(t+1) = s_j\left(1-G_j(t)\right)N_j(t) + \frac{Y_j V_j(t) G_j(t) N_j(t)}{C'(t)} \qquad (1)$$

Thus, the density of the seeds of species j in the seed bank, $N_j(t+1)$, at the beginning of year $t + 1$ is equal to the sum of the seeds that persist in the seed bank, $s_j(1 - G_j(t))N_j(t)$, plus production of new seed, which is the second term in equation (1). New seed production requires germination, G, survival and growth, V, but is of course limited by competition.

Competition, $C'(t)$, needs to be defined to represent how much growth is restricted by the demands placed on resources. Under lottery competition, each individual receives resources in proportion to its ability to extract them, which is assumed here to be proportional to the vigor of its growth. Assuming that the resources are limited, and are all used by these species, each individual is limited in its growth by the total ability (per unit area) of all seedlings of all species to extract those resources. This means that the resources received by an individual are proportional to $V_j(t)/C'(t)$, with $C'(t)$ defined as the sum over species of the total density of seedlings weighted by the vigor of their growth:

$$C'(t) = \sum_{l=1}^{n} V_l(t) G_l(t) N_l(t) .$$

The quantity $V_j(t)G_j(t)N_j(t)/C'(t)$ is assumed to be the biomass of growing plants of species j. Multiplying by Y_j converts this biomass into the number of new seeds of species j produced per unit area.

Vigor, $V_j(t)$, deserves special mention. It is not the actual average mass of a plant, but the final mass of a plant at flowering when $C'(t)$ is fixed at the minimal value of 1. It is intended as a measure of how strongly the physical environment in year t promotes survival and growth of the plants, and therefore how much demand they place on resources — hence their role in $C'(t)$. Vigor is not directly observable in nature. Only the actual average mass, $V_j(t)/C'(t)$, is observable. However, in equation (1) only the ratios of vigor for different species are needed, and these are observable. The particular observable related to vigor that is measured in this study is per germinant fecundity, here equal to $Y_j V_j(t)/C'(t)$. The time by species interaction of ln per germinant fecundity, which features in our analysis, is exactly equal to the time by species interaction of ln vigor, as discussed below.

To analyze the model, we focus on the growth rate, $r_j(t)$, which is defined as $\ln[N_j(t+1)/N_j(t)]$, i.e. the log of the finite rate of increase. For the model (1), this growth rate is

$$r_j(t) = \ln\left\{s_j\left(1-G_j(t)\right) + Y_j V_j(t) G_j(t)/C'(t)\right\}. \qquad (2)$$

In other words, it is the natural log of the sum of per capita seed bank persistence, and per germinant fecundity. The theory of population dynamics in variable environments emphasizes that it is the sum of $r_j(t)$ over time that determines population trajectories on the log scale (e.g. Chesson (3)), because population growth is multiplicative, and becomes additive on a log scale. Note also that key components of the model are multiplicative, under the assumption that nature works multiplicatively. In particular, per germinant fecundity equals $Y_j V_j(t) G_j(t)/C'(t)$, a product of four quantities. Transforming these quantities to the log scale (natural log, ln) converts this product into a sum. This transformation has two effects. First it greatly simplifies the formal mathematical analysis of the model following the procedures of Chesson(1, 3), and second it separates per germinant fecundity into additive terms amenable to statistical analysis by standard techniques.

To see how the storage effect coexistence mechanism arises from this model, we now formally define the environmental responses of the species. These are population parameters that vary with the physical environment in ways that differ between species, and thus separate their niches temporally. The correlations between species in their environmental responses thus need to be less than 1. There are two environmental responses in our development $E_{Gj}(t) = \ln G_j(t)$ and $E_{Vj}(t) = \ln V_j(t)$, together with their combination $E_j(t) = E_{Gj}(t) + E_{Vj}(t)$. There is, however, but a single competitive response, $C(t)$, measuring the effect of competition on population growth, which is the natural log of competition, C', defined above, i.e.

$$C(t) = \ln\left\{\sum_l V_l(t) G_l(t) N_l(t)\right\}. \qquad (3)$$

All of these responses use the log scale to facilitate the theoretical calculations and statistical analysis, as explained above.

The storage effect coexistence mechanism arises from the interactions between competitive response and the environmental responses in the way they determine $r_j(t)$. Fundamentally, persistence of dormant seeds in the seed bank provides a buffer against unfavorable conditions for seed production as defined by poor germination, low vigor, or high competition. This means that a species does not have to be successful every year to persist in the system. Success, however, involves the occurrence of favorable combinations of environmental and competitive conditions, which is especially important when a species has become depressed to low density and is to increase and recover from that low-density state. In the formal mathematical analysis, called invasibility analysis, such a species is called an *invader*. Other species not depressed to low density are called *residents.*

The concept of covariance between environment and competition helps us understand how an invader achieves a favorable combination of environmental and competitive conditions. Looking at the formula (3) for competition, it is quite clear that if a species does experience favorable environmental conditions, viz the combination of germination and vigor are high, then it contributes more to $C(t)$, which then places limitations on its own growth. However, because it is at low density, this effect is small. Of more concern is competition from other species, but if these species have environmental responses not strongly correlated with those of the invader, they will not always contribute strongly to $C(t)$ when the invader is favoured by the environment. Mathematically, this means that the invader has low covariance between environment and

competition. In terms of population growth of an invader, it means that the invader will have times when it is favored both environmentally and competitively, and so can increase strongly.

It is important that these same opportunities are not as frequently available for the resident species, because then they would create levels of competition high enough to deprive the invader of an average population growth advantage. However, residents, being at higher density, do limit their own growth by competition when favored by the physical environment. The higher demands they place on resources do add up to important increases in competition. This means residents have strong positive covariance between environment and competition, leaving invaders at an average advantage. The storage effect thus depends on invader-resident differences in covariance between environment and competition (which provide opportunities for invader increase) and buffered population growth (which means that times of decrease cannot cancel out the long-term effects of strong periods of growth). The mathematical theory of the storage effect(1, 3) makes these ideas precise and quantitative. We show now how this theory is applied to the model in this paper.

Previous theory has considered just a single environmental response, and so needs to be extended to consider the interaction between competition and both environmental responses in the sense of how they jointly contribute to the growth rate r_j. These considerations lead to two distinct storage-effect contributions to coexistence. Although it has no effect on the final result, we analyze the model using the two environmental responses $E_{Gj}(t)$ and $E_j(t)$. Any two of three above would give the same outcome. Some developments of the storage effect standardize the environmental responses before analysis, as described in Chesson(3). For simplicity, the development here is in terms of the original environmental and competitive responses, defined

above, rather than in terms of the more formal procedure standardizing these responses(3). These two approaches are equivalent, given appropriate care(4).

The development begins with a quadratic approximation of r_j in G_j, V_j, and C^* about equilibrial values, G_j^*, V_j^* and C^*, for which $r_j = 0$. We find below that we need to specify only one of these equilibrial values, viz G_j^*, which is set at the species and time average germination fraction. The others play no role in the final result. We need also the important quantity $\beta_j = 1 - s_j(1 - G_j^*)$ which is the equilibrial probability that a seed leaves the seed bank ("the seed loss rate"). Note that β_j is equal to $-\partial r_j / \partial C$ evaluated at the equilibrial parameter values. Next we need the interaction terms,

$$\gamma_j = \frac{\partial^2 r_j}{\partial E_j \partial C} = -\beta_j(1-\beta_j), \tag{4}$$

and

$$\gamma_{Gj} = \frac{\partial^2 r_j}{\partial E_{Gj} \partial C} = -s_j G_j^* \beta_j, \tag{5}$$

both evaluated at the equilibrial values. These quantities define the extent to which population growth is buffered against unfavorable environmental conditions. Large negative values mean strong buffering.

We can now proceed to use these quantities to calculate the community average storage effect(1, 5). The community average storage effect indicates how strongly the storage effect promotes coexistence in terms of its average effect on increasing long-term low-density growth rates, $\overline{r_i}$ (1). These are the average of $r_i(t)$ over time for a species i in the invader state, and define

how strongly species *i* recovers from low density. A positive value of $\overline{r_i}$ means that the species recovers in the long run, and remains in the community.

Here the community average storage effect has two components, one for each environmental response. We first calculate this component for the response E_j. From Chesson(5), the community average storage effect is

$$\overline{\Delta I} = \frac{1}{n}\sum_{j=1}^{n}\frac{\gamma_j}{\beta_j}\left(\chi_j^{\{-j\}} - \overline{\chi_j^{\{-i\}}}^{\{i\neq j\}}\right). \qquad (6)$$

In this expression χ_j = cov(E_j,C) (covariance between environment and competition), taken over time. The superscript {–*l*} indicates that this measurement is taken for species *l* (either *i* or *j* in (6)) in the invader state, as discussed in Chesson(1, 5). The bar with {$i\neq j$} indicates the average over all *i* except *j*.

These covariances are now approximated using the techniques in Chesson(3), which maintain accuracy so that errors are of a smaller order of magnitude than the storage effect terms being approximated, provided the variances of the environmental responses are not too large. See Chesson(3) for details. The competitive response is approximated linearly in the form

$$\tilde{C} = \sum\nolimits_{u\neq i} A_u^{\{-i\}}\tilde{E}_u + b\,. \qquad (7)$$

Here ~ indicates that the equilibrial value has been subtracted from the response. The quantities $A_u^{\{-i\}}$ and *b* are random variables independent of the $\tilde{E}_u$. Defining $a_u^{\{-i\}} = E\left[A_u^{\{-i\}}\right]$, where E[…] means expected value taken according to the probability distribution over time (a time average), and χ_{ij} = cov(E_i, E_j), we see that

$$\chi_j^{\{-i\}} = \sum_{u \neq i} a_u^{\{-i\}} \chi_{ju} \ . \qquad (8)$$

Now Chesson(3) appendix VI shows that $a_u^{\{-i\}}$ is equal to the expected fraction of the seedling biomass attributed to species *u* when species *i* is in the invasion state. It follows that $\chi_j^{\{-i\}}$ is a weighted average of the χ_{ju} and can be approximated by the simple average

$$\chi_j^{\{-i\}} = \overline{\chi}_{ju}^{\{u \neq i\}}, \qquad (9)$$

with error term equal to the covariance over resident species,

$$\varepsilon_j^{\{-i\}} = \mathrm{cov}_{\{u \neq i\}} \left((n-1) a_u^{\{-i\}}, \chi_{ju} \right). \qquad (10)$$

This error cannot be large except in the unlikely event of strong average dominance correlated with the environmental covariances.

Based on equation (9), the community average storage effect is approximated by

$$\frac{1}{n} \sum_{j=1}^{n} \frac{\gamma_j}{\beta_j} \left(\overline{\chi}_{ju}^{\{u \neq j\}} - \overline{\overline{\chi}_{ju}^{\{u \neq i\}}}^{\{i \neq j\}} \right), \qquad (11)$$

which simplifies to

$$\frac{1}{n} \sum_{j=1}^{n} \frac{\gamma_j}{\beta_j} \left(\frac{\overline{\chi}_{ji}^{\{i \neq j\}} - \chi_{jj}}{n-1} \right). \qquad (12)$$

This result leads to the approximation

$$\overline{\Delta I} \approx \frac{\overline{(\gamma / \beta)}}{n-1} \sum_{j=1}^{n} \left(\frac{\overline{\chi}_{ji}^{\{i \neq j\}} - \chi_{jj}}{n} \right) \qquad (13)$$

with error term again a covariance over species and equal to

$$\delta = \mathrm{cov}_j\left(\frac{\gamma_j}{\beta_j}, \frac{\overline{\chi}_{ji}^{\{i\neq j\}} - \chi_{jj}}{n-1}\right), \tag{14}$$

which is likely to be dominated by expression (13) in most circumstances. Moreover, the data on the species studied here do not show statistically differences in γ_j/β_j. Hence, it is expression (13) that we use for the community average storage effect.

The quantity $\overline{\chi}_{ji}^{\{i\neq j\}} - \chi_{jj}$ can be written as

$$-\frac{n}{n-1}E\left[\left(E_j - E[E_j]\right)\left(E_j - E[E_j] - \overline{E}. + E[\overline{E}.]\right)\right] \tag{15}$$

where $\overline{E}.$ is the average of E_j over j, and all expected values are taken over time (each E_j is a function of time). Because the sum over j of $\left(E_j - E[E_j] - \overline{E}. + E[\overline{E}.]\right)$ is zero, the average over j of (15) is equal to

$$\begin{aligned} &-\frac{1}{n-1}\sum_{j=1}^{n} E\left[\left(E_j - E[E_j] - \overline{E}. + E[\overline{E}.]\right)\left(E_j - E[E_j] - \overline{E}. + E[\overline{E}.]\right)\right] \\ &= -\frac{1}{n-1}\sum_{j=1}^{n} E\left[\left(E_j - E[E_j] - \overline{E}. + E[\overline{E}.]\right)^2\right], \end{aligned} \tag{16}$$

which is the negative of the theoretical time by species variance, $\sigma_{t\times s}^2$, combining germination and vigor. Thus, the community average storage effect for germination and vigor combined is approximated as

$$\overline{\Delta I} \approx \frac{\overline{(-\gamma/\beta)}\sigma_{t\times s}^2}{n-1} = \frac{\left(1-\overline{\beta}\right)\sigma_{t\times s}^2}{n-1} \tag{17}$$

The community average storage effect component for germination separately follows identically, but with χ_{ij} = cov(E_{Gi}, E_j). At the final stage, expression (16) is replaced by

$$-\frac{1}{n-1}\sum_{j=1}^{n} E\left[\left(E_{Gj}-E[E_{Gj}]-\bar{E}_{G}.+E[\bar{E}_{G}.]\right)\left(E_{j}-E[E_{j}]-\bar{E}.+E[\bar{E}.]\right)\right]$$

which is the negative of the time by species covariance between germination and its combination with vigor on the log scale, designated $\chi_{G,GV,t\times s}$. Thus, this storage effect component is

$$\overline{\Delta I} \approx \frac{\overline{sG}\chi_{G,GV,t\times s}}{n-1}. \qquad (18)$$

(Note that the subscripts *G*, *V* and *GV* here are short hand for E_G, E_V and $E = E_G + E_V = \ln(GV)$, here and below. This should cause no confusion as the analysis is on the log scale throughout.)

Partitioning of the storage effect into functional components

The time by species variance, $\sigma^2_{t\times s}$, splits into three components.

$$\sigma^2_{t\times s} = \sigma^2_{G,t\times s} + 2\chi_{G,V,t\times s} + \sigma^2_{V,t\times s} \qquad (19)$$

corresponding to the time by species variance in ln germination fraction, twice the time by species covariance between ln germination fraction and ln vigor, plus the time by species variance in ln vigor. Similarly, the covariance $\chi_{G,GV,t\times s}$ splits into two components

$$\chi_{G,GV,t\times s} = \sigma^2_{G,t\times s} + \chi_{G,V,t\times s}. \qquad (20)$$

We can use these decompositions to rearrange the storage-effect contributions into

$$\overline{\Delta I}_G \approx \frac{s\sigma^2_{G,t\times s}}{n-1}, \tag{21}$$

due to variance in ln germination fraction alone,

$$\overline{\Delta I}_{G,V} \approx \frac{\overline{s}(2-\overline{G})\chi_{G,V,t\times s}}{n-1}, \tag{22}$$

due to the covariance between ln germination fraction and ln vigor (equivalently ln per germinant fecundity), and

$$\overline{\Delta I}_V \approx \frac{\left(1-\overline{\beta}\right)\sigma^2_{V,t\times s}}{n-1} \tag{23}$$

due to the variance in ln vigor.

As mentioned above, the data *analysis* uses per germinant fecundity, not vigor. However ln (per germinant fecundity) = ln V_j (t) + ln Y_j. The fact that Y_j does not depend on time means that it disappears from the time by species interaction for ln per germinant fecundity, leaving only ln vigor. Hence the per germinant fecundity can be substituted for vigor in the above expressions without changing the result.

Each of the quantities above represents an increase in the average over species (average over i) of the long-term low-density growth rate, $\overline{r_i}$, of the species in the system due to that particular variance or covariance component, measured with time unit, 1/β, which is the average time for the loss of a seed from the seed bank. This measurement is on the *natural timescale*(5) of seed generations, which is the most appropriate timescale for comparing organisms with

different life-histories. To convert these to contributions to per year rates, they are each multiplied by $\overline{\beta}$.

Time by species interactions and correlation coefficients

From the derivation of the community average storage effect, we know that the time by species interaction variance is equal to

$$\frac{1}{n}\sum_{j=1}^{n}\left(\chi_{jj}-\overline{\chi}_{ji}^{\{i\neq j\}}\right). \tag{24}$$

Now $\chi_{jj}=\sigma_j^2$, the variance of $E_j(t)$ over time, and $\chi_{ji}=\rho_{ji}\sigma_j\sigma_i$, where ρ_{ji} is the temporal correlation between $E_j(t)$ and $E_i(t)$. Therefore, equation (24) becomes

$$\overline{\sigma^2}-\overline{\rho}\left\{\frac{1}{n(n-1)}\sum\nolimits_{i\neq j}\sigma_i\sigma_j\right\}, \tag{25}$$

where $\overline{\sigma^2}$ is the species average variance, and $\overline{\rho}$ is the weighted average correlation,

$$\overline{\rho}=\sum\nolimits_{i\neq j}\rho_{ij}\sigma_i\sigma_j\Big/\sum\nolimits_{i\neq j}\sigma_i\sigma_j\ . \tag{26}$$

A little algebra shows that

$$\frac{1}{n(n-1)}\sum\nolimits_{i\neq j}\sigma_i\sigma_j=\overline{\sigma^2}-\frac{1}{n-1}\sum\nolimits_j\left(\sigma_j-\overline{\sigma}\right)^2, \tag{27}$$

so that the time by species covariance reduces to

$$\overline{\sigma^2}\left(1-\overline{\rho}\right)+\frac{\overline{\rho}}{n-1}\sum\nolimits_j\left(\sigma_j-\overline{\sigma}\right)^2. \tag{28}$$

The key term here is,

$$\overline{\sigma^2}\left(1-\overline{\rho}\right). \qquad (29)$$

Added to this is the average correlation times the variance over species in the temporal standard deviation. If these standard deviations are similar, i.e. the species are about equally sensitive to environmental variation, on average, then expression (29) defines the time by species interaction. Expression (29) provides an intuitive understanding of the time by species interaction. It represents the time by species interaction as that part of the average variance that is independent between species, partitioning out the common fraction of variance, $\overline{\rho}$, leaving the fraction that is unique to a species, $1-\overline{\rho}$. This partitioning is the essence of equation (24), but the precise form of the partitioning of variance is slightly different when different species have different variances, leading to the correction term that is added in equation (28). As the calculations here use the time by species interaction directly, they include this correction term. However, the approximation (29) provides the intuition behind this concept in the section on the workup of the empirical data.

Quantification of the magnitude of the storage effect. In the first scenario described in the main text, species coexistence is promoted if a set of species produce persistent seed banks with variable germination fractions that are not completely correlated(6). A second scenario involves temporal variation in the vegetative phase (i.e., post-germination growth and reproduction) of the life cycle. Here we partition the storage effect into these two mechanisms and their covariance. The formulae for magnitude of the storage effect, and its division into these three components,

are derived above (see *Derivation of the community average storage effect*) using the technique of quadratic approximation of Chesson 1994(3) and the community average approach of Chesson 2003(1). As mentioned above, the community average approach for quantifying coexistence is appropriate because coexistence is a community-level property. The component measures for the community average storage effect indicate how much the low density growth rates of the species are increased, on average, by the mechanism in question. These results are given on the per generation time scale, which is the reciprocal of the rate, β, at which seeds are lost from the seed bank. They are thus the amounts by which $\overline{r}/\beta$ is increased on average. To convert these to per year rates, i.e. to $\overline{r}$, one just multiplies by β, which here has the average value of 0.77.

The storage effect component for germination is

$$\overline{\Delta I}_G \approx \frac{\overline{s}\sigma^2_{G,t\times s}}{n-1} \qquad (30)$$

where $\overline{\Delta I}_G$ is the symbol for this component of the community average storage effect, $\overline{s}$ is the average survival rate of ungerminated seeds in the seed bank, $\sigma^2_{G,t\times s}$ is the time by species interaction variance component for ln germination fraction, and n is the number of species. A more intuitive formula is given in terms of the average temporal correlation between species, $\overline{\rho}_G$, and average temporal variance, $\overline{\sigma^2_G}$, in ln germination fraction:

$$\overline{\Delta I}_G \approx \frac{\overline{s}\,\overline{\sigma^2_G}\left(1-\overline{\rho}_G\right)}{n-1} \qquad (31)$$

which is valid whenever the temporal variances do not vary too greatly between species, as derived above. ***The quantity*** $\overline{\sigma^2_G}\left(1-\overline{\rho}_G\right)$ ***is an approximation to*** $\sigma^2_{G,t\times s}$***, which shows that it and***

the storage effect are driven by low correlations between species on average, and high variance over time.

The contribution of per germinant fecundity to the storage effect is

$$\overline{\Delta I}_V \approx \frac{\left(1-\overline{\beta}\right)\sigma^2_{V,t\times s}}{n-1} \tag{32}$$

where $\sigma^2_{V,t\times s}$ is the species by time interaction component of variance for ln per germinant fecundity, ln(*lb*), and 1- $\overline{\beta}$ is the average probability that a seed in the seed bank neither germinates nor dies in a given year. Like ln germination fraction, this formula can be approximated by the more intuitive formula,

$$\overline{\Delta I}_V \approx \frac{\left(1-\overline{\beta}\right)\overline{\sigma^2_V}\left(1-\overline{\rho}_V\right)}{n-1}. \tag{33}$$

A third contribution to the storage effect is due to the species by time interaction for the covariance of log germination fraction and log per germinant fecundity:

$$\overline{\Delta I}_{G,V} \approx \frac{\overline{s}(2-\overline{G})\chi_{G,V,t\times s}}{n-1} \tag{34}$$

where $\chi_{G,V,t\times s}$ is the time by species covariance component for ln germination and ln per germinant fecundity, and $\overline{G}$ is the average germination fraction, taken over all species. A more interpretable approximation in terms of average covariances and correlations analogous to (31) and (32) above is available here too.

Sixteen years of long-term data on germination fraction(7) and the corresponding sixteen years of demographic data described in the **Materials and Methods** were used to calculate values of these parameters (Table S1). The species x time interaction was highly significant for ln-transformed germination, per germinant reproduction and their covariance ($P < 2.8$ E-21, $P <$ 5 E-06, $P < 2.7$ E-10). The low-density population growth advantage due to germination variation is calculated to be $\overline{\Delta I}_G = 0.067$. This means that the storage effect contributed by this germination mechanism boosts the $\overline{r} / \beta$ value by 6.7% per generation or boosts $\overline{r}$ by 5.2%, in essence multiplying the finite rate of increase by 1.052. The low-density advantage due to reproductive variation is $\overline{\Delta I}_V = 0.032$ (Table S2). The low-density advantage due to covariation of germination and reproduction is an additional $\overline{\Delta I}_{G,V} = 0.035$, making the total direct and indirect contribution of species by year interaction for reproduction equal to $\overline{\Delta I} = 0.133$, which means a substantial boost to growth equal to a 10.3% population growth rate advantage for species at low density.

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Supporting Information

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Table S1. Parameter estimates for calculating the magnitude of the storage effect

Parameter	Value
Species x time variance component for germination	1.46
Species x time variance component for per germinant fecundity	1.27
Species x time covariance component for germination and fecundity	0.49
Average survival of ungerminated seeds, $\bar{s}$	0.41
Average germination fraction	0.45
Average rate of loss from the seed bank, $\bar{\beta}$	0.77
Number of species	10

These are the parameters for Eqs. **30**, **32**, and **34** (*SI Appendix*) and are calculated from demographic data on winter annual plants at the University of Arizona Desert Laboratory (see *Materials and Methods*).

Table S2. Partitioning of the low-density log growth rate from the storage effect

Mechanism	Boost to $\bar{r}/\beta$	Boost to $\bar{r}$
Germination Variation	0.067	0.052
Reproduction Variation	0.032	0.025
Covariation of Germination and Reproduction	0.035	0.027
Total	0.133	0.103

Storage effect is partitioned into parts due to germination variation, reproductive variation, and the covariation of germination and reproduction calculated with Eqs. **30**, **32**, and **34** in *SI Appendix*.

Table S3. Demographic difference matrices

	ERCI	*ERLA*	*ERTE*	*EVMU*	*PERE*	*PLIN*	*PLPA*	*SCBA*	*STMI*
ERCI		1.57	0.86	2.47	1.02	1.02	1.39	1.11	1.04
ERLA	0.52		2.51	2.91	2.62	1.29	1.20	1.67	1.38
ERTE	0.05	0.89		3.90	1.96	0.85	1.54	2.17	2.72
EVMU	0.29	0.03	0.59		4.72	2.50	1.76	2.29	1.39
PERE	0.09	1.02	0.00	0.69		2.64	2.18	3.07	2.39
PLIN	0.03	0.77	0.00	0.49	0.02		1.12	1.46	1.48
PLPA	0.01	0.63	0.02	0.38	0.05	0.01		1.85	1.56
SCBA	0.32	0.02	0.63	0.00	0.74	0.53	0.41		1.23
STMI	0.19	0.08	0.45	0.01	0.54	0.36	0.26	0.02	

Species-by-year squared difference matrix given in upper diagonal. Species-by-precipitation squared difference matrix given in lower diagonal. Species abbreviations are the first two letters of the genus and specific epithet given in *Materials and Methods*.

Table S4. Functional trait difference matrices

	ERCI	*ERLA*	*ERTE*	*EVMU*	*PERE*	*PLIN*	*PLPA*	*SCBA*	*STMI*
ERCI		3.95	0.21	9.60	0.30	2.57	0.68	7.30	12.55
ERLA	4.12		5.99	1.23	2.08	0.15	1.35	0.51	2.42
ERTE	0.10	5.53		12.66	1.01	4.25	1.65	10.00	16.02
EVMU	16.51	4.14	19.24		6.51	2.24	5.17	0.16	0.20
PERE	1.90	11.61	1.11	29.61		1.12	0.08	4.65	8.98
PLIN	0.00	4.12	0.10	16.51	1.90		0.61	1.21	3.76
PLPA	0.11	2.90	0.42	13.96	2.91	0.11		3.53	7.39
SCBA	2.58	0.18	3.71	6.05	8.90	2.57	1.63		0.71
STMI	4.29	0.00	5.73	3.97	11.90	4.29	3.04	0.22	

Squared differences in principal component I score for analysis of variation in RGR and Δ are given in upper diagonal. Squared differences in principal component I score for analysis of variation in 5 key traits (Nleaf, LMR, Jmax:VCmax, SLA and RGR plasticity) are given in lower diagonal. Species abbreviations are the first two letters of the genus and specific epithet given in *Materials and Methods*.

Table S5. Comparison of results with and without phylogenetic distance correction

Functional trait difference matrix	Demographic difference matrix	Mantel *P* value	Partial Mantel *P* value
5 key traits	Species × year interaction	0.0003	<0.001
RGR-Δ	Species × year interaction	0.0410	0.048
5 key traits	Species × precip interaction	0.0068	0.009
RGR-Δ	Species × precip interaction	0.0453	0.042

Results are shown for partial Mantel tests calculated in the R package vegan with a phylogenetic distance matrix based on equal branch lengths. Results using a phylogenetic distance matrix based on pseudo branch length differences were qualitatively identical.

Other Supporting Information Files

SI Appendix