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E-Article

Coexistence and Coevolution in Fluctuating Environments: Can the Storage Effect Evolve?

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abstract: Both theoretical and empirical work have shown that the temporal storage effect can promote coexistence. However, the storage effect depends on temporally fluctuating demographic rates, such as interannually variable germination rates. Because variable demographic rates often reduce fitness, we asked how a storage effect might evolve. Using a model of competing annual plants, we find that variable germination (and hence a storage effect) can evolve only if germination is positively correlated with high-fecundity years (predictive germination) or if one species has limited ability to evolve. Outside of these conditions, the storage effect is evolutionarily unstable: if two species were thrown together with traits that would permit a storage effect, they would coevolve constant germination rates and the storage effect would vanish. Our results suggest that for the temporal storage effect to be widespread, either germination must commonly be positively correlated with later growth or fecundity or community assembly must reflect biogeographic processes more than they do coevolution.

Keywords: coevolution, environmental variation, predictive germination, storage effect.

Introduction

Theoretical ecologists have invested decades in elaborating classes of coexistence mechanisms. A next step is to consider whether the combinations of traits required by these mechanisms represent evolutionarily stable strategies. If the strategies are stable, they would represent an end point for coevolution and community assembly. On the other hand, if a mechanism is based on unstable strategies, populations with the requisite traits thrown together during community assembly might coexist only transiently, until selective pressures ultimately erode the means by which they coexist. Coexistence mechanisms that depend on temporal fluctuations in the environment may be especially likely to involve traits that incur selective costs.

As previous authors have observed (Higgins et al. 2000; Adler and Drake 2008), the idea that high variation in an important demographic rate might have a positive effect on population growth runs counter to a large body of theory developed from single-species models. When variation in demographic rates produces variation in year-to-year population growth, a species' long-run growth rate is reduced because of the geometric averaging of population growth rates over time (Lewontin and Cohen 1969; Boyce 1992; Menges 2000). This cost is always present and can select against variability in demographic rates that have a strong influence on fitness (Morris et al. 2008; Dalgleish et al. 2010). The cost of variability explains why annual plants in a randomly varying environment with no predictive germination are expected to germinate a constant fraction of their seeds (Cohen 1966).

Variable demographic rates may still evolve if there are benefits to set against the cost of a variable growth rate. For example, if germination is positively correlated with establishment or fecundity (either through active detection of environmental cues or because both processes depend on similar environmental requirements), then variable germination yields a benefit as a well as a cost. If the correlation is sufficiently strong, there may be selection for variable germination rates (Cohen 1967).

Further benefits of variability are possible when we consider a species within a community, where variable demographic rates can permit a species to avoid competition. This idea is at the heart of the storage effect, the most studied of the fluctuation-dependent mechanisms (Chesson and Warner 1981; Chesson and Huntly 1989; Chesson 1994), now known to operate in some aquatic and terrestrial communities (Caceres 1997; Adler et al. 2006; Angert et al. 2009). The storage effect promotes coexistence when species' demographic rates fluctuate in response to variable environmental conditions and these demographic

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rates covary in a way that helps species reduce their competition with each other. For example, for two competing annual species to avoid head-to-head competition, one species might have a high germination rate in warm years and a low germination rate in cool years, while its competitor's germination rate would vary in the opposite direction with temperature. In this way, variance in germination rates can play a key role in increasing species' long-run low-density growth rates.

Our goal was to identify the conditions under which a storage effect can evolve—that is, how variable germination can evolve—using the classic case of a storage effect that depends on variable germination rates. We used an adaptive-dynamics framework to analyze a well-studied model of two competing annual plant species (Watkinson 1980; Chesson and Huntly 1989). We asked how the evolution of variance in each species' germination rate depends on correlations in germination between species and correlations between germination and fecundity within species (predictive germination). Our results show that on their own, the benefits of avoiding competition are not sufficient to overcome the cost of variable growth rates. The storage effect can evolve only if germination is positively correlated with fecundity or if only one species is able to evolve.

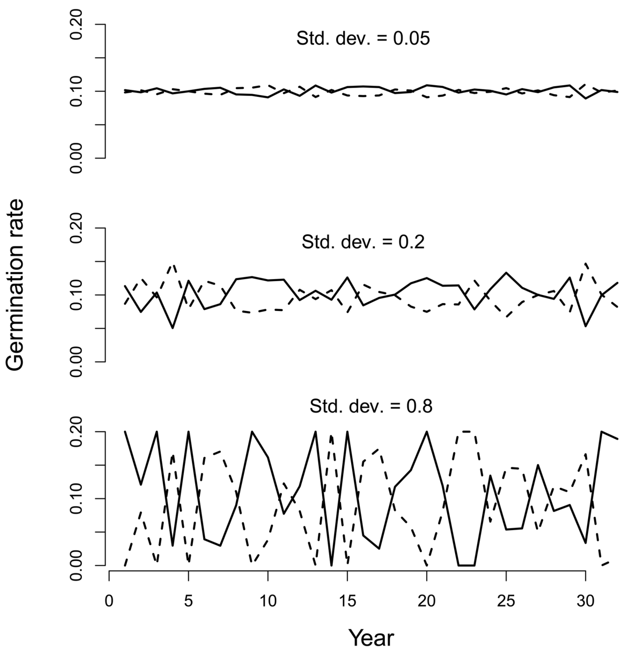

Figure 1: Example germination time series for different levels of variation. Note that even though the two species have their highest germination rates in different years ($\mathrm{Corr}(g_1, g_2) = -1$), there is still substantial overlap in their germination times unless the standard deviation is quite high.

Modeling Framework

Model

We consider two species of annual plants. Because of environmental fluctuations, their fecundity varies from year to year, and their germination fractions may vary as well. We assume that fluctuations in fecundity are unavoidable and possibly species specific (e.g., some plants may be more productive in years with cool springs and others in warm springs) but that variance in germination fraction is subject to selection.

The two species may have similar germination triggers, in which case germination fluctuations for the two species will be positively correlated, or they may have different triggers, yielding a negative correlation. We consider the two extremes of perfectly correlated and perfectly anticorrelated germination time series. Even anticorrelated germination fluctuations typically result in significant overlap between the two species (fig. 1), but peak germination times are offset, and so a storage effect is possible. No storage effect is possible if germination is perfectly correlated.

Germination may also be positively correlated with fecundity. We consider correlations ranging from 0 (no prediction) to 1 (perfect prediction).

For the results shown here, both fecundity and germination fluctuations are modeled as Gaussian white noise: the value of fecundity or germination in one year is not correlated with the values in succeeding years. We have also considered fecundity and germination time series with positive temporal autocorrelation ("red" or "pink" noise); however, positive autocorrelation had little effect, and so we do not include those results.

The number of seeds of species j at time t is given by $n_j(t)$. In year t, a proportion $g_j(t)$ of seeds germinates. Those that do not germinate survive until the following year with probability s_j, so that the fraction of dormant seeds is $s_j(1 - g_j(t))$. Adults can produce up to $F_j(t)$ seeds; however, seed production is reduced by competition ($C_j(t)$), so that the actual number of seeds produced is $F_j(t)/C_j(t)$. The competition experienced by species j from species k is equal to the number of species-k adults ($g_k(t)n_k(t)$) times the competition coefficient representing the effects of species k on species j (γ_{jk}). Summing over both species, then,

$$C_j(t) = \gamma_{j1} g_1(t) n_1(t) + \gamma_{j2} g_2(t) n_2(t). \tag{1}$$

Putting everything together, our population dynamics are given by

$$n_j(t+1) = \frac{g_j(t)F_j(t)}{C_j(t)} n_j(t) + s_j(1 - g_j(t))n_j(t)$$
$$= \lambda_j(t)n_j(t), \tag{2}$$

where $\lambda_j(t) = g_j(t)F_j(t)/C_j(t) + s_j(1 - g_j(t))$.

For our standard parameter set, we assume that species 1 has higher average fecundity ($\langle F_1\rangle_t = 200$, $\langle F_2\rangle_t = 160$) but that species 2 is a superior competitor ($\gamma_{12} = 1$, $\gamma_{21} = 0.5$). We also assume that each species competes with itself at least as strongly as it competes with the other ($\gamma_{22} = 1$, $\gamma_{11} = 0.7$). This parameter set exemplifies a typical fecundity-competition trade-off. In addition, we consider the situation in which species compete more strongly with each other than with themselves ($(\gamma_{12} = 1) > (\gamma_{22} = 0.4)$, $(\gamma_{21} = 1) > (\gamma_{11} = 0.55)$). As we explain in "Results," this parameter set gives us the strongest possibility of seeing a storage effect evolve in the absence of a positive correlation between germination and fecundity but makes coexistence exceedingly fragile. These two parameter sets represent the two possibilities that appendix C tells us should be important: within-species competition stronger than between-species competition and vice versa.

Both species have high survival within the seed bank ($s_1 = s_2 = 0.9$, giving a mean lifetime in the seed bank of 9 years), and both have a time-averaged germination fraction of 10%: $\langle g_1\rangle_t = \langle g_2\rangle_t = 0.1$. This high level of dormancy favors the evolution of a storage effect and thus represents a conservative assumption with respect to our conclusion that the storage effect is difficult to evolve. For both species, $\mathrm{Var}(F_j) = 0.1\langle F_j\rangle_t^2$.

Finding the Evolutionarily Stable Germination Variance

To find the evolutionarily stable (ES) coevolved germination variances, we first find the ES germination variance of species 1 as a function of the variance of species 2 and then find the ES germination variance of species 2 as a function of the variance of species 1. Where the two optimality curves intersect, neither species will be driven to change its germination strategy in response to the other, and these two variances will represent an ES coalition.

In order to find, for example, the ES germination variance of species 1 as a function of the variance of species 2, we consider coexisting populations of species 1 and 2, with germination variances $\mathrm{Var}(g_1)$ and $\mathrm{Var}(g_2)$, respectively. To these "resident" populations we add an "invader" population of species 1, identical to the resident species 1 in every way except that the invader has germination variance $\mathrm{Var}(g_i)$. If the invader has higher fitness than its conspecific resident, it takes over and becomes the new resident, subject to new would-be invaders. The process stops when the best variance an invader could choose would be to match the conspecific resident variance. This is the ES species 1 variance for that species 2 variance. We therefore need an expression for invader fitness, which is defined as the long-run growth rate of the invader, $\bar{r}_i$.

Defining Fitness

While the full invader fitness can be found only by simulation, we have an analytic approximation that is valid for small fluctuations in germination and fecundity. The details of the derivation we leave to appendix A, but we provide an overview here because it gives some insight into the ways that variation can both decrease and increase long-run growth.

We assume that fluctuations in fecundity and germination are small relative to their means and for all species j write

$$F_j(t) = \langle F_j\rangle_t(1 + f_j(t)), \tag{3}$$

$$g_j(t) = \langle g_j\rangle_t(1 + \Omega_j(t)), \tag{4}$$

where f_j and Ω_j are $O(\sigma)$.[1] Small fluctuations in fecundity and germination produce correspondingly small fluctuations in competition:

$$C_j(t) = \langle C_j\rangle_t(1 + c_j(t)), \tag{5}$$

where $c_j(t)$ is $O(\sigma)$. The yearly growth rate $\lambda_j(t)$ is a nonlinear function of fecundity and germination and so can be Taylor expanded to $O(\sigma^2)$ as

$$\lambda_j(t) \approx \lambda_j^{(0)}\left(1 + \zeta_j^{(1)}(t) + \zeta_j^{(2)}(t)\right), \tag{6}$$

where $\lambda_j^{(0)}$ represents the growth rate in the absence of fluctuations, $\zeta_j^{(1)}(t)$ is linear in the fecundity and germination fluctuations, and $\zeta_j^{(2)}(t)$ is quadratic in the fluctuations.

The long-run growth rate $\bar{r}_j$ is equal to the time average of the logarithm of the yearly invader growth rates: $\bar{r}_j = \langle \ln \lambda_j(t)\rangle_t$. Substituting in equation (6) for λ_j and expanding to $O(\sigma^2)$, we find that

$$\bar{r}_j = \left\langle \ln \lambda_j^{(0)} + \zeta_j^{(1)} + \zeta_j^{(2)} - \frac{1}{2}\zeta^{(1)^2} \right\rangle_t$$
$$= \ln \lambda_j^{(0)} + \langle \zeta_j^{(2)}\rangle_t - \frac{1}{2}\langle \zeta^{(1)^2}\rangle_t. \tag{7}$$

The first term ($\ln \lambda_j^{(0)}$) represents long-run growth in the absence of fluctuations. The second term ($\langle \zeta_j^{(2)}\rangle_t$) represents the increase or decrease in long-run growth caused

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[1] The technical definition of $O(\sigma^n)$ is that if $g(x)$ is $O(\sigma^n)$, then $g(x)$ decreases with σ and $|g(x)/\sigma^n|$ can be made less than or equal to some positive constant K for small enough σ. On a more practical note, σ is some measure of smallness that we use to keep track of the order of approximation.

by the fact that yearly growth λ_j is a nonlinear function of germination and fecundity; call this "intrinsic nonlinearity." For this model, intrinsic nonlinearity increases long-run growth. The last term $(-(1/2)\langle\zeta^{(1)^2}\rangle_t)$ represents the decrease in long-run growth caused by the fact that long-run growth is a nonlinear function (ln) of yearly growth; call this "discrete-time nonlinearity."

Using population dynamics equations (eqq. [1], [2]) and focusing specifically on the invader (subscript *i*), we can find expressions for $\zeta_i^{(1)}$ and $\zeta_i^{(2)}$ and reach an expression for the invader long-run growth rate:

$$\begin{aligned}\bar{r}_i = \ln\lambda^{(0)} &+ \underbrace{A_1(\mathrm{Cov}(\Omega_i, f_i) - \mathrm{Cov}(\Omega_i + f_i, c_i) + \mathrm{Var}(c_i))}_{\text{intrinsic nonlinearity}}\\ &\underbrace{-\frac{1}{2}A_1^2(\mathrm{Var}(\Omega_i + f_i) - 2\,\mathrm{Cov}(\Omega_i + f_i, c_i) + \mathrm{Var}(c_i)) - \frac{1}{2}A_2^2\,\mathrm{Var}(\Omega_i)}_{\text{discrete-time nonlinearity}}\\ &\underbrace{-A_1A_2(\mathrm{Var}(\Omega_i) + \mathrm{Cov}(\Omega_i, f_i) - \mathrm{Cov}(\Omega_i, c_i))}_{\text{discrete-time nonlinearity}},\end{aligned} \tag{8}$$

where A_1 and A_2 are positive constants. We can also reorder the terms to make the contributions of predictive germination and the storage effect more apparent:

$$\begin{aligned}\bar{r}_i = \ln\lambda^{(0)} &+ \underbrace{(A_1 - A_1^2 + A_1A_2)\,\mathrm{Cov}(\Omega_i, f_i)}_{\text{predictive germination}}\\ &\underbrace{-(A_1 - A_1^2)\,\mathrm{Cov}(\Omega_i + f_i, c_i) - A_1A_2\,\mathrm{Cov}(\Omega_i, c_i)}_{\text{storage effect}}\\ &+\underbrace{\left(A_1 - \frac{1}{2}A_1^2\right)\mathrm{Var}(c_i)}_{\text{relative nonlinearity}}\\ &\underbrace{-\frac{1}{2}(A_1 - A_2)^2\,\mathrm{Var}(\Omega_i) - \frac{1}{2}A_1^2\,\mathrm{Var}(f_i).}_{\text{fluctuation penalty}}\end{aligned} \tag{9}$$

Predictive germination and the storage effect increase long-run population growth and fitness, while the fluctuation penalty decreases long-run growth. We have also labeled the contribution from relative nonlinearity, a coexistence mechanism described in Chesson (1994). While this term does increase long-run growth, it does not depend on variation in the invader germination rate and provides no selective pressure, so we do not discuss it further.

Note that there are two potential storage effects that we discuss. Here, we are discussing coevolution and so are considering coexisting populations of species 1 and 2, plus an invader that is a mutant form of either species. A negative covariance between environment (fluctuations in invader fecundity and germination) and competition (exerted by both resident species on the invader) will increase invader fitness and select for increased variance in germination. However, we also wish to think about the implications for species coexistence, in which case we want to know whether a species reduced to low density will be able to grow back in the presence of its competitor species: that is, a single resident of one species and an invader of the other species. Clearly, the competition exerted by both species will not be the same as the competition exerted by a single species, and so these two storage effects are not the same. However, both rely on variable germination rates. If variable germination cannot coevolve, then the storage effect cannot promote species coexistence.

Results

Here we examine not just the conditions under which a germination-based storage effect can evolve but the evolution of variable germination more generally.

As germination becomes more correlated with fecundity, ES germination variance increases. As we move to the right in figure 2, germination fluctuations become more strongly correlated with fecundity fluctuations and the ES germination variance increases for both species. Plants that germinate more seeds in years when they will be excep-

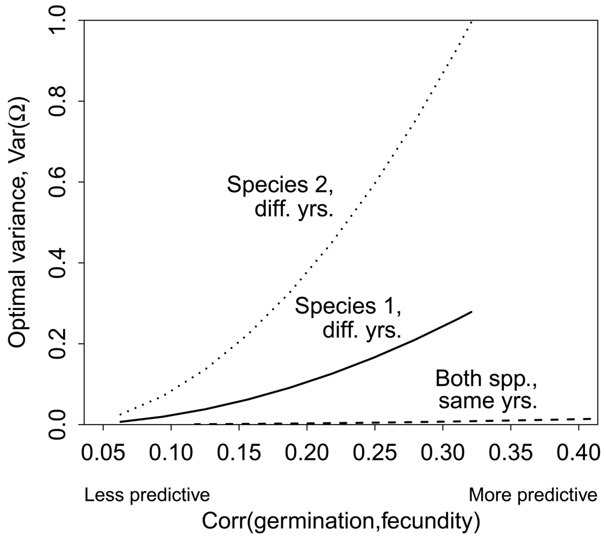

Figure 2: Evolutionarily stable germination variances when species have their highest germination rates in different years or the same years ($\mathrm{Corr}(g_1, g_2) = -1$ or $\mathrm{Corr}(g_1, g_2) = 0$). For all figures, the variance in fecundity is 10% of the squared mean for each species. (Caveat: the curves become less accurate as the predicted variance increases, and so all plots should be interpreted qualitatively, not quantitatively.)

tionally fecund as adults will increase in frequency under natural selection, to the extent that this tendency has a genetic basis. (Caveat: our analytic approximation is a perturbation approach, with variance as the small parameter. Our approximation becomes less accurate as variance becomes large, so the curves in figure 2 should be interpreted qualitatively, not quantitatively: germination variance increases as germination becomes more correlated with fecundity, but we cannot say precisely by how much.)

If species have their highest germination rates in the same years, even perfectly predictive germination ($\mathrm{Corr}\,(g, F) = 1$*) selects for only a small germination variance.* ES germination variance never gets very large when species have their peak germination in the same years (fig. 2). Since the two species increase their germination in the same years, the benefit of germinating in a high-fecundity year is offset by increased competition.

It is very difficult for a storage effect to coevolve if germination is not positively correlated with fecundity. The storage effect promotes coexistence most strongly when species' germination fluctuations are anticorrelated. Because the species have their peak germination in opposing years, an invader will experience the least competition precisely when its germination rate is highest and so will get a large boost. Looking at figure 2, however, we see that without a positive correlation between germination and fecundity, variable germination does not evolve, and so there can be no storage effect.

To understand what is happening, let us consider the expression for fitness given by equation (9). There is no predictive germination, so we can ignore that set of terms. Relative nonlinearity does not depend on invader germination, so that is constant, as is, of course, $\ln \lambda^{(0)}$, the growth rate in the absence of variation. That leaves two terms by which the invader's germination variance can affect fitness: the "fluctuation penalty," which becomes more negative as invader germination variance increases, and the storage effect. If increasing invader germination variance decreases the invader's exposure to whichever resident exerts the greater amount of competition, then $\mathrm{Cov}\,(\Omega_i, c_i)$ will decrease, the storage effect will increase, and fitness will be determined by the contest between the fluctuation penalty and the storage effect, possibly peaking at some nonzero variance. However, if increasing invader germination variance increases the invader's exposure to the main source of competition, then $\mathrm{Cov}\,(\Omega_i, c_i)$ will increase and the fitness will decrease monotonically. Thus, if fitness is to peak at some nonzero invader variance for both species, increasing invader variance must decrease both invaders' exposure to competition.

The only way this can happen is if the between-species competition coefficients are greater than the within-species competition coefficients, that is, if each species limits the other more than it limits itself. We offer a mathematical argument in appendix C. The intuitive argument, however, is as follows. To understand how increasing invader germination variation will affect the invader's exposure to competition, we need to remember that when we consider coevolution, we are considering an invader in the presence of both conspecific and heterospecific residents. The invader has peak germination times at the same time as the conspecific resident; they are the same species and have the same germination triggers. As we increase invader germination variance, the invader germinates more of its seeds (higher peaks) during the peak conspecific resident germination times, increasing its exposure to the conspecific resident. On the other hand, as we decrease invader germination variance, making germination more uniform, we increase the invader's exposure to the heterospecific resident, for we have assumed that the two residents have their peak germination times in opposing years. If the storage effect is to increase with invader variance, then both invaders must experience less competition when they increase their exposure to the conspecific resident (and decrease their exposure to the heterospecific resident). That means that each species must limit itself less than it limits the other species (fig. 3).

Of course, it is difficult for species to coexist under these conditions. And indeed, while our analytic approximation predicts that the species should coevolve very small but nonzero germination variances when the between-species competition coefficients exceed the within-species competition coefficients (fig. 3*d*), simulations with the full nonlinear equations indicate that once germination begins to vary, one species will eventually be excluded.

Note that if one species' variance were fixed, the other would evolve a nonzero variance (fig. 4). In this case, whichever species is evolving finds that some variance in germination is adaptive, even in the absence of a positive correlation between germination and fecundity. However, when the two species coevolve without such a correlation, there is no pair of variances that is evolutionarily stable for both species, and their variances ratchet down to 0.

Discussion

We found that the storage effect, and the germination variance it depends on, can evolve via natural selection, but only under restrictive scenarios. A positive correlation between germination and fecundity was the most important requirement, leading to low levels of germination variance when species' germination rates were perfectly correlated and higher germination variance when competitors' germination rates were anticorrelated (producing a temporal storage effect). Without a correlation between germination and fecundity, the storage effect evolved only

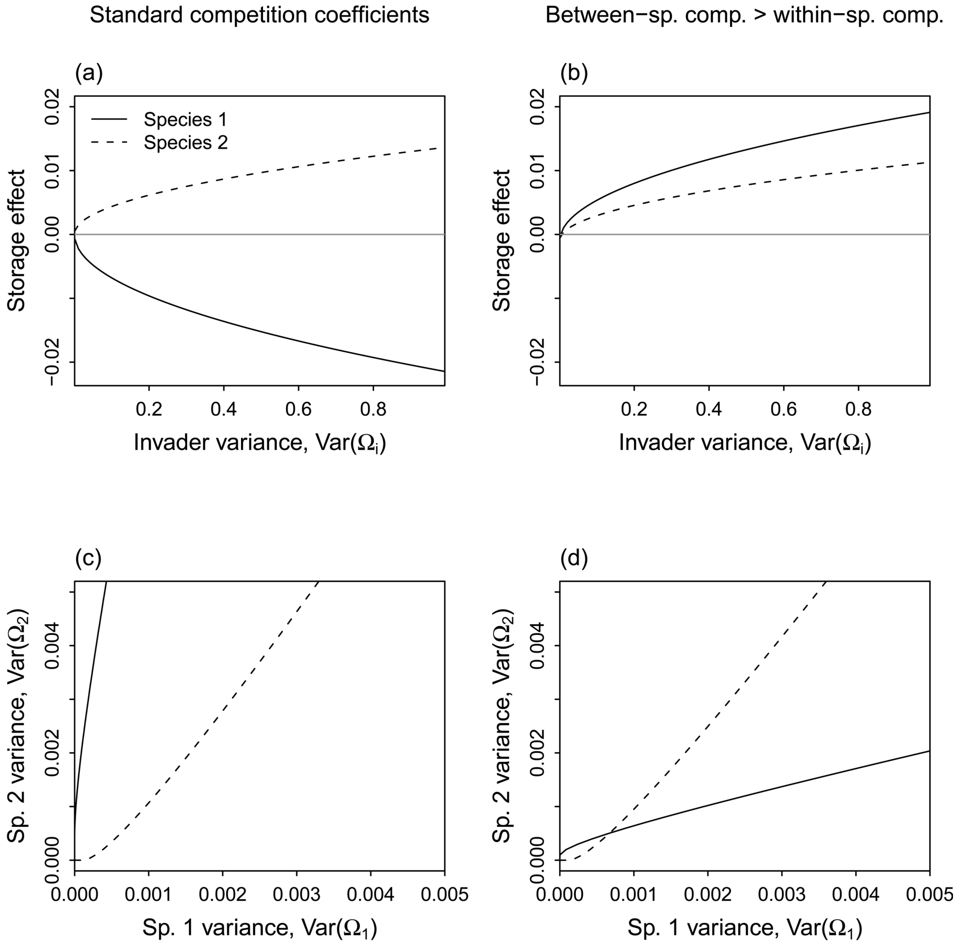

Figure 3: Effects of changing the competition coefficients. In all panels, there is no predictive germination (Corr(g_j, F_j) = 0), and species have their highest germination rates in opposing years (Corr(g_1, g_2) = −1). The standard competition coefficients ($\gamma_{12} = \gamma_{22} = 1$, $\gamma_{21} = 0.5$, $\gamma_{11} = 0.7$) were used for *a* and *c*. In *b* and *d*, the between-species competition coefficients are larger than the within-species competition coefficients (($\gamma_{12} = 1) > (\gamma_{22} = 0.4)$, $(\gamma_{21} = 1) > (\gamma_{11} = 0.55)$). *a*, With the standard competition coefficients, the storage effect increases with invader germination variance for one species and decreases for the other. *b*, As a result, the optimal variance curves for species 1 and 2 fail to intersect except at the origin, so that the coevolved variances are both 0. *c*, When the between-species competition coefficients are larger than the within-species competition coefficients, the storage effect increases with invader germination variance for both species. *d*, As a result, the optimal variance curves do intersect, albeit at a very small variance, so that the coevolved variance is nonzero.

with unrealistic intra- and interspecific competition coefficients or if one species' traits were fixed. Indeed, without a correlation between germination and fecundity (and without assumptions of unrealistic competition coefficients or fixed traits), the storage effect is evolutionarily unstable: if two species were thrown together with traits that would permit a storage effect, they would coevolve constant germination rates and the storage effect would vanish.

How common is a positive correlation between germination and later growth or fecundity? One way for a positive correlation to arise is through actively predictive germination. According to theory, predictive germination should evolve if the cost to a plant of "sensing" environmental cues is not too high (Cohen 1967; Ellner 1985). Tagkopoulos et al. (2008) show that the cost of evolving predictive behavior is surprisingly low in both randomly evolving networks and microbes. While this work may not apply directly to more complex organisms, perhaps we should not be surprised that predictive germination has been observed in a number of annual-plant communities (Venable et al. 1993; Tielborger and Valleriani 2005; Levine et al. 2008) and that even more impressive predictive behavior has been documented in vertebrates (Orians and

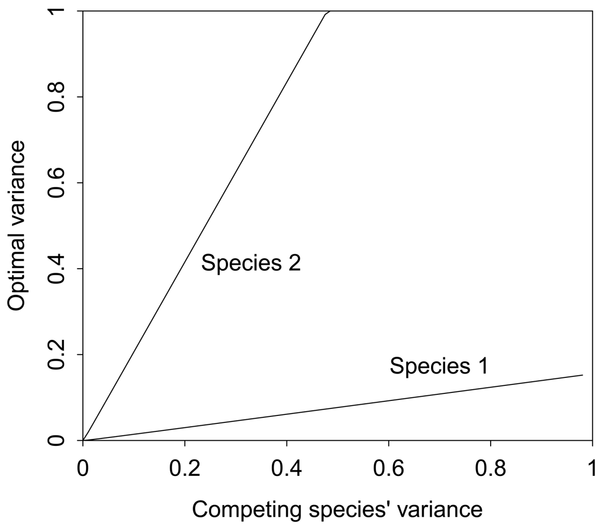

Figure 4: Evolutionarily stable variance when only one species can evolve. The "species 1" curve shows the optimal species 1 germination variance for a given, fixed species 2 variance; vice versa for the species 2 curve. The species have their highest germination rates in different years, but there is no predictive germination ($\mathrm{Corr}(g_1, g_2) = -1$, $\mathrm{Corr}(g_j, F_j) = 0$ for $j = 1, 2$).

Wittenberger 1991; Boutin et al. 2006). In addition, correlations may arise without mechanisms to detect environmental cues. Jongejans et al. (2010) found significant positive correlations among vital rates in 11 of the 40 perennial plant species they analyzed. Such correlations might simply reflect the influence of environmental variables on multiple vital rates.

In the absence of a positive correlation between germination and later growth or fecundity, the storage effect could evolve in two ways. First, as discussed in "Results," our analytic approximation indicates that variable germination should be possible for a narrow parameter range in which within-species competition is weaker than between-species competition. However, species coexistence is extremely fragile when species limit others more than themselves, and when we simulate the full nonlinear dynamics, we find that the species cannot coexist in a variable environment under these conditions.

The second way the storage effect might evolve without correlations between germination and other processes is if one species has limited ability to change its germination strategy, so that only one species is evolving freely. For example, founder effects can limit genetic variation (Amsellem et al. 2000), as can selfing (Charlesworth and Charlesworth 1995) or a previous history of strong selection (Blows and Hoffmann 2005 and references therein). Furthermore, evolution may be impeded if selection acts in incompatible ways on traits that are genetically correlated ("antagonistic" correlations; Blows and Hoffmann 2005).

What if a storage effect is present but germination is not correlated with future growth or fecundity and there are no apparent constraints on the evolution of either species? It is worth considering the possibility that the observed storage effect is transient. If evolutionary timescales are slower than ecological timescales, then it is possible that a species with the right traits could enter a community and persist there for a time via a gradually eroding storage effect.

While it is always possible that there are selective pressures that our model does not include, our results seem likely to generalize. For example, the evolution of a storage effect may be even more problematic in natural, multispecies systems than in the two-species model we analyzed. Just as in the two-species model, the key is for an increase in germination variation to decrease the invader's exposure to competition. However, it will be more difficult to avoid competition with multiple competitors germinating on multiple schedules (Chesson 1994). Even if invader germination variance does decrease all invaders' exposure to competition, the resulting decrease may be quite small. In this case, the usual penalty of a time-varying growth rate may outweigh any slight reduction in competition.

While our model focuses on variable germination in annuals, our results should generalize to other life-history strategies. In a classic storage effect, an organism can store the gains of favorable years in the form of a seed bank, a seedling bank, adult stem tissue, and so on. These storage states are insensitive to poor environmental conditions as well as to competition. In order to grow, however, the stored material must be mobilized, at which point it may become vulnerable to unfavorable environmental conditions and competition. If mobilization occurs while competitors are less active, so that stored benefits are used when interspecific competition is weakest, a storage effect is possible. Our arguments about variable germination should generalize to variation in any form of mobilization, for example, meristem activation in perennials (Chesson et al. 2004).

While the analogy is less direct, our arguments should also generalize to less traditional forms of the storage effect, such as one that relies on fluctuations in seedling establishment probability. Regardless of the specific demographic transition where variability occurs, increases in variability will increase exposure to conspecific competition and decrease exposure to heterospecific competition (assuming anticorrelated demographic rates). Unless species limit each other more than themselves or there is some other benefit to variation, selection will work against demographic variability and the storage effect.

Our analysis relies on adaptive dynamics, which carries its own set of assumptions (Geritz et al. 1998; Waxman and Gavrilets 2005). Beneficial mutations are assumed to increase in frequency (genetic drift is ignored), and mutations are assumed to be rare enough that the population will reach an attractor before a new mutation arises. Furthermore, mutations are assumed to produce small changes in phenotype. We have assumed asexual reproduction in our analysis, but some of the greatest effects of sexual reproduction occur when there are branching points (Waxman and Gavrilets 2005), which did not occur in our mode.

Our results suggest that coevolution may work against storage-effect-induced coexistence in many situations. Other studies have also found that coevolution may diminish the likelihood of coexistence. Egas et al. (2004) and Ravigné et al. (2009) have shown that evolution can reduce the ability of two specialists and a generalist to coexist. Likewise, coexistence via life-history trade-offs can collapse when traits not directly related to competitive ability are allowed to evolve (Mougi and Nishimura 2007). On the other hand, one of us has found that in a spatiotemporally fluctuating environment, coexistence between annuals and perennials is almost always more robust when seed dispersal distances are allowed to coevolve than when dispersal traits are kept at their monoculture values (R. E. Snyder, unpublished data). More broadly, Urban and Skelly's (2006) review notes both positive and negative examples of coevolution on coexistence.

In conclusion, while the storage effect can be a highly effective mechanism of coexistence, we found that it is not evolutionarily stable without positive correlations between germination and later growth or fecundity or constraints on the evolvability of some species. Where storage effects have been observed in terrestrial (Adler et al. 2006; Angert et al. 2009) and aquatic systems (Caceres 1997), these conditions are likely present. Indeed, Angert et al. (2009) did observe both a storage effect and a positive correlation between germination and reproduction in their study of desert annuals. Our results highlight the need for more research on positive correlations between germination and other traits, whether they are due to common environmental influences or to evolved predictive mechanisms. Observations of such predictive behavior could be used to test our theory and to help identify communities with a high potential for strong temporal storage effects. More generally, we urge consideration of how likely a coexistence mechanism is to evolve. If certain coexistence mechanisms are common despite predictions that they should be difficult to coevolve, then community assembly may reflect biogeographic processes more than coevolution.

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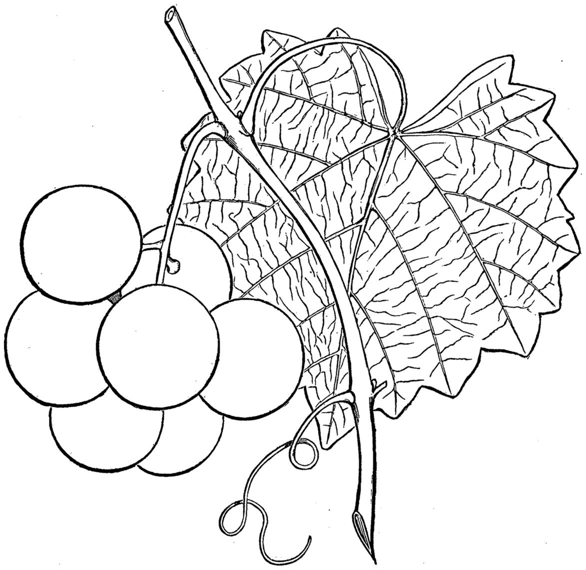

Southern muscadine grape *Vitis rotundifolia.* “The berries ... are brown-black and shining when commencing to ripen but a dull-black, dotted and sometimes blotched with red when fully ripe. They vary much on different vines, being sometimes hard and sour, but often tender and deliciously sweet. In the best specimens the pulp finally dissolves, and the skins become literally bags of wine.” From “The Southern Muscadine Grape” by D. H. Jacques (*American Naturalist*, 1868, 1:638-641).