EVOLUTION OF THE STORAGE EFFECT

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The storage effect, a mechanism that promotes species coexistence in temporally variable environments, poses a dilemma to evolutionary ecologists. Ecological studies have demonstrated its importance in natural communities, but evolutionary models have predicted that selection either impedes coexistence or diminishes the storage effect if there is coexistence. Here, we develop a lottery model of competition in which two species experience a trade-off in competitive ability between two types of years. We use an adaptive evolution framework to determine conditions favoring the evolution of the storage effect. Storage evolves via divergence of relative performance in the two environments under a wide range of biologically realistic conditions. It evolves between two initially identical species (or lineages) when the trade-off in performance is strong enough. It evolves for species having different initial trade-offs for both weak and strong trade-offs. Our simple 2-species-2-environment scenario can be extended to multiple species and environmental conditions. Results indicate that the storage effect should evolve in a broad range of situations that involve a trade-off in competitive ability among years, and are consistent with empirical observations. The findings show that storage can evolve in a manner and under conditions similar to other types of resource partitioning.

The storage effect (Chesson, 1994) is a mechanism for the coexistence of competing species in temporally varying environments. Chesson (1994) and Chesson et al. (2004) identify three components of the storage effect: (1) temporal differences between species in their per capita competitive abilities; (2) persistence through unfavorable periods; and (3) positive temporal covariation of periods of high growth potential and low competition. The first and third components are largely determined by how different environmental conditions affect the utilization rates of the limiting resource by two (or more) competing species. When two species have different relationships between utilization rate of a resource and one or more varying environmental factors, a rare species can achieve a high per capita growth rate under conditions that allow it to have a much greater utilization rate and/or competitive ability than its competitor(s). As Chesson (2003, p. 345) pointed out, the storage effect "is a formalization of the concept of temporal niche differentiation."

Most theory on the storage effect has focused on its ecological role in promoting coexistence (Chesson 2000), and has shown that it can support coexistence of many species (Chesson 1994). Similarly, empirical studies provide many examples of coexistence via the storage effect (Caceres 1997; Adler et al. 2006; Angert et al. 2009). Nevertheless, it appears that only two theoretical studies have explored the evolution of the storage effect (Kisdi and Meszéna 1995; Snyder and Adler 2011). Kisdi and Meszéna (1995) examined the evolution of trade-offs between survival and reproductive investment in the basic lottery model. They concluded that evolution of such traits most often inhibited local coexistence, frequently producing alternative single-species outcomes. Recently, Snyder and Adler (2011) explored a more narrowly defined model of competing annual plants; they argued that evolution decreased variation in germination, eliminating a storage effect if one already exists. Increased variance could only evolve if germination was positively correlated with performance during the later competitive stage, or if one species had little or no ability to evolve a different germination variance. Snyder and Adler (2011, p. E76) conclude that: "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."

These two, largely negative views of the effect of evolution on the storage effect contrast with analyses of the effect of traditional character displacement, which generally allows or strengthens coexistence (Abrams 1996). This is true for both nutritionally substitutable resources (Lawlor and Maynard Smith 1976; Taper and Case 1985, 1992; Abrams 1986) and nutritionally essential or complementary resources (Abrams 1987b; Fox and Vasseur 2008; Vasseur and Fox 2011). Such contrasting evolutionary effects are not expected, given that the storage effect is a form of temporal resource partitioning (Chesson 2003).

The storage effect involves several components, so there are several ways in which it could be altered by evolution. Here, we examine the evolution of traits determining species' abilities to use resources under different environmental conditions, when those conditions vary temporally. We employ a version of Chesson and Warner's (1981) original lottery competition model, in which the environmental variation affects reproduction. An adult stage provides the between-year "storage" of competitive effects needed for coexistence.

We show that storage evolves by increases in a consumer's ability to use resources under some environmental conditions at the expense of its ability to use resources under other conditions. The resulting change in the temporal pattern of competition in each species is a simple analog of character divergence in resource utilization rates in deterministic models of resources that are present simultaneously. Species that coexist due to mechanisms other than storage and those that already experience a storage effect also undergo evolution in their temporal pattern of performance that creates and/or increases the storage effect when they become sympatric. In the 2-species model considered here, the evolution of the storage effect increases the temporal variation in both fitness and population densities in at least one, and often both species.

Models and Analysis

Competition is represented by a simple lottery model similar to those used by Chesson and Warner (1981). Recruitment of young is the competitive stage of the life history, and is also the stage when temporal variation in performance occurs. Different species must have different responses of their offspring production rates to a variable environmental factor to coexist. Given this basic scenario, the storage effect increases if the temporal correlation of different species' per capita offspring production decreases as the result of evolution. This article shows that such a decrease is expected under adaptive evolution, given trade-offs in competitive performance in different environments.

Our basic model represents the dynamics of a given competitor type, where the "competitor type" can be either a species or a reproductively isolated lineage within a species; we refer to both as "species." The adult population size $N_i(t)$ of species i at time t changes based on:

$$N_i(t+1) = \frac{\lambda a_i(t) N_i(t)}{\sum_{all\,species\,j} a_j(t) N_j(t) + \varepsilon} + s_i N_i(t), \quad (1)$$

where $a_i(t)$ is the per capita "competitive ability" of species i at time t. Competitive ability could be the per capita rate of uptake of a limiting resource or rate of production of reproductive propagules. Using the latter interpretation, the parameter λ is the maximum summed recruitment rate of all competing species. The annual survival probability of adults is s. The recruitment function is a Beverton–Holt curve, where ε represents the amount of competition (ΣaN) at which total births are half the maximum value. In many previous studies ε is set to zero, implying an abundance of seeds/larvae sufficient to produce the maximum recruitment in all years. Under the original lottery model, λ is the number of settlement sites opened up by the death of adults; in this case, its value is proportional to $(1 - s)$.

The first term in equation (1) may also represent competitive consumption of food that is required for reproduction, and regenerates according to chemostat dynamics (Abrams 1984; Rueffler et al. 2006). In this case, $a_i(t)$ represents an attack rate (per capita consumption rate by one consumer i individual), λ represents the product of the input rate of the resource and the consumer's conversion efficiency (with the latter equivalent for all species), and ε represents the per capita washout or loss rate of the resource.

Our analysis concentrates on a simple type of environmental variation; a random sequence of equally probable years that have either of two different sets of conditions (years of type 1 or type 2). Equation (1) still describes the dynamics, but the competitive ability of species i (a_i) can be recast as a function of year type (denoted z; $z = 1$ or 2) and of the trait, x_i (with $0 \leq x_i \leq 1$), which determines the relative ability of species i individuals to compete in the two environments. Performance in the competitive stage is independent of the environment type if $a_i(x_i, 1) = a_i(x_i, 2)$. Given equal maximum a values for each type of year, and a scenario with "mirror image" effects of the trait on a_i in each type of year, $x = 1/2$ satisfies this condition. There is no temporal variation in competition if x is fixed at 1/2. If $x \neq 1/2$, competitive performance differs from year to year; types may be better at recruitment in years of type 2 and worse in years of type 1 (if $x < 1/2$), or better in type 1 years if $x > 1/2$.

In most of the following analysis, we assume that the competitive ability ($a_i(x, 1)$) of an individual with trait x in a year of type 1 is given by $A_{i1}f(x)$, and the competitive ability in years

of type 2 is $A_{i2}f(1 - x)$, where A_{ij} is the maximum competitive ability of species i in type-j years, and f is an increasing function with $f(0) = 0$ and $f(1) = 1$. Completely specialized individuals ($x = 0$ or 1) have zero competitive ability in year types 1 and 2, respectively. The trade-off is symmetrical when $A_{i1} = A_{i2}$. Larger values of x increase production of recruits in type 1 years and decrease production in type 2 years. Recruit production reflects an individual's ability to take up resources and/or convert them to offspring, as well as offspring survival to the adult stage. We follow Rueffler et al. (2006) in describing the trade-off as strong when $f'' > 0$ and weak when $f'' < 0$, where primes denote derivatives. Weak trade-offs imply that a generalist ($x = 1/2$) has a competitive ability greater than the average of the two specialists (see Fig. 1 below). We will not consider cases where curvature, f'', changes sign with x.

The evolution of x is described by the gradient dynamics that arises from quantitative genetic models of frequency dependent traits with a low genetic variance (Iwasa et al. 1991; Abrams et al. 1993). Because of the frequency dependence, the fitness gradient in this equation is formulated in terms of the fitness of a rare "mutant" type within species i having a trait x_{iM} that differs slightly from the "resident" trait, x_{iR}. The assumption here is that, as in traditional models of quantitative genetics, recombination maintains a relatively narrow and unimodal distribution of trait values (see, e.g., Schreiber et al. 2011). The change in the trait over 1 year is:

$$\Delta x_i = v_i x_{iR}(1 - x_{iR})(\partial W_i(x_{iM}, x_{iR})/\partial x_{iM}|_{x_{iM}=x_{iR}})/W_i(x_{iR}, x_{iR}), \tag{2}$$

where $W_i = s + \lambda A_{i1}f(x_{iM})/(\varepsilon + A_{i1}f(x_{iR})N_i)$ in a type 1 year and $W_i = s + \lambda A_{i2}f(1 - x_{iM})/(\varepsilon + A_{i1}f(1 - x_{iR})N_i)$ in a type 2 year; v_i is a rate constant for evolutionary change, and is proportional to the additive genetic variance. The product, $x_{iR}(1 - x_{iR})$ on the right-hand side of the equation reflects the loss of genetic variation implied as the mean resident trait approaches a maximum or minimum value (Abrams 1999). The rate constant v_i may be interpreted as four times the maximum additive genetic variance (which occurs when $x_{iR} = 1/2$). Similar results (P. A. Abrams, unpubl. data) were obtained using an alternative model (Abrams and Matsuda 2004) in which genetic variance is approximately constant for most trait values, but biased mutation prevents x from too closely approaching its limiting values of 1 and 0. Appendix S1 analyzes the attractivity of the intermediate and boundary states for a symmetric 1-species model; these results are applied below.

THE OUTCOME OF EVOLUTION IN A SINGLE SPECIES
We begin by analyzing single species evolution, as this is a prerequisite for understanding the evolution of two competitors. The
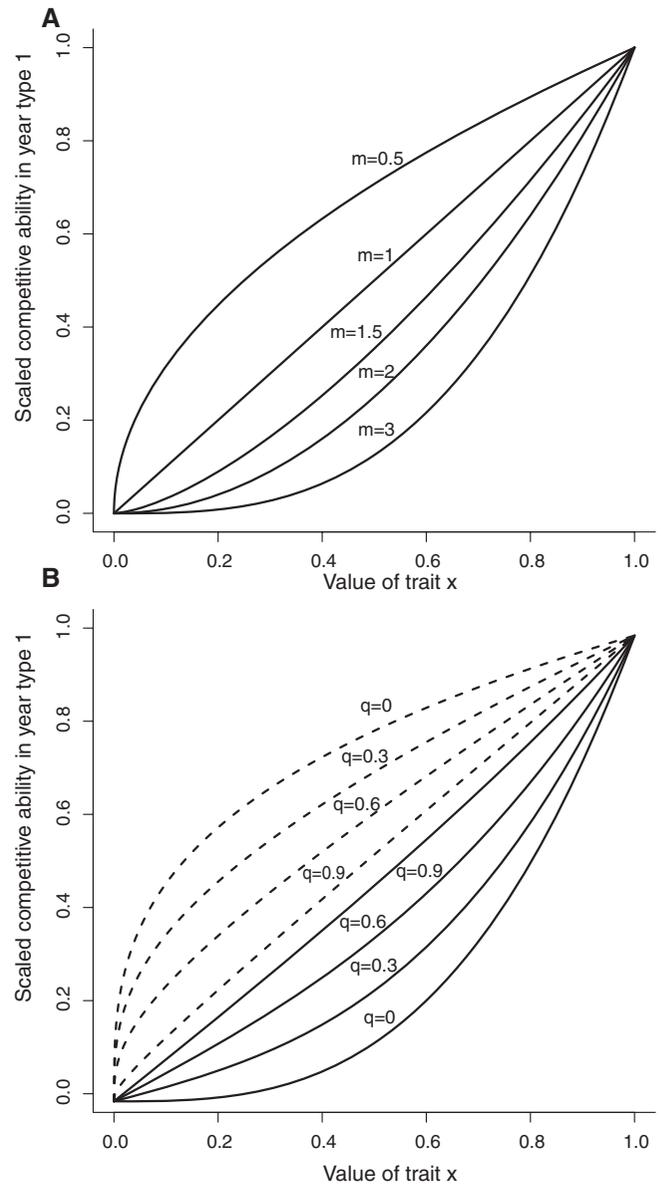
Figure 1. The functional forms of the trade-off in competitive ability considered in the examples provided. **(A)** The pure power-law trade-off. Values of the trade-off exponent (*m*) greater than 1 produce a strong trade-off in which a specialist strategy has a greater (arithmetic) mean competitive ability than a generalist strategy. **(B)** The binomial trade-off function, shown with a varying linear component (*q*) for a weak trade-off (*m* = 0.33, dashed lines) and a strong trade-off (*m* = 3, solid line). Competitive ability is given for a year type 1; competitive ability for year type 2 is the same as shown here with the *x*-axis reversed (i.e., running from 1 to 0).

single species, and our initial assumption that the trade-off is symmetrical, allow us to drop all subscripts. Consider the generalist equilibrium at $x = 1/2$. Rearranging equation (A-2) in Appendix S1, the condition for local stability of the generalist

state with slow evolution is:

$$\frac{\varepsilon s(1-s)}{A\lambda} < \left(1 - \frac{f\,f''}{f'^2}\right) f,\qquad(3)$$

where primes denote derivatives of f, which are evaluated at the equilibrium ($x = 1/2$). This inequality sets bounds on the shapes of the trade-off that allows the generalist equilibrium to evolve with a symmetric trade-off. The generalist state is always local attractive when $\varepsilon = 0$ and $f'^2 > ff''$. The latter inequality involving f and its derivatives is satisfied for all parameters given either a power-law trade-off or the binomial trade-off introduced below; in addition, it must be satisfied for any weak trade-off. The condition $\varepsilon = 0$ corresponds to the assumption that all empty sites are filled (or resources used) every year. This in turn allows the per capita reproductive output to become arbitrarily large when N is sufficiently low. In a 2-species competitive system, $\varepsilon = 0$ results in an extremely strong rare-type advantage when the two types have different environmental sensitivities. In most natural systems, a nonzero value of ε is likely; some resources are lost from the system due to processes other than consumption or some empty sites are not located. Thus, we use a small positive value for the recruitment half-saturation value ε in the numerical examples below. If $\varepsilon > 0$, the shape of f determines stability of the generalist equilibrium; sufficiently strong trade-offs make $x = 1/2$ an evolutionary repeller.

The generalist equilibrium may coexist with one or two locally attractive specialist equilibria; conditions for their local stability are also presented in Appendix S1. In general, both the trait and the population size fluctuate in any system for which $\varepsilon > 0$. However, fluctuations in both variables become very small when x is close to 1/2 and the evolutionary response is slow (v is

probability s. The generalist state is then least likely to be stable when survival is high.

Determining the dynamics of the system requires a specific form for the scaled trade-off function, f. The most common form is a simple power law: $f(x) = x^m$. Here, $m > 1$ is a strong and $m < 1$ is a weak trade-off. Under a symmetric power-law trade-off, $x = 1/2$ represents a fitness maximum provided that $m < 1/s$; it is a locally attracting state for all exponents that satisfy this condition (see Appendix S1). However, $x = 1/2$ can also represent a locally attracting evolutionary state for a range of strong trade-offs (larger exponents), as shown below. Larger values of m make it less likely that a generalist will evolve, as they imply a greater disadvantage for generalists relative to specialists. The power function trade-off may often be unrealistic, as it implies that very large decreases in the competitive performance of a near-specialized type are required to achieve extremely small increases in its performance on the other year type. Thus, we also investigate a binomial function consisting of a linear and a nonlinear term: $f(x) = qx + (1-q)x^m$, where q is a positive constant ($0 < q < 1$). This function preserves the sign of second derivative of f. However, positive q means that f has a positive slope at $x = 0$. Figure 1 illustrates some trade-offs with power function and binomial forms.

If the phenotypic distribution within the population remains unimodal with a small variance, the dynamics are described by the following two equations, which assume the binomial f, and are based on equations (1) and (2) above, with the environment denoted by z:

$$N_{t+1} = \begin{cases} N_t \left(\dfrac{\lambda A_{11}\left(qx_t + (1-q)x_t^m\right)}{\varepsilon + A_{11}N_t(qx_t + (1-q)x_t^m)} + s \right) & \text{if } z = 1 \\[2em] N_t \left(\dfrac{\lambda A_{12}(q(1-x_t)+(1-q)(1-x_t)^m)}{\varepsilon + A_{12}N_t(q(1-x_t)+(1-q)(1-x_t)^m)} + s \right) & \text{if } z = 2 \end{cases}$$

(4a)

$$x_{t+1} = \begin{cases} x_t + vx_t(1-x_t)\left(\dfrac{\lambda A_{11}\left(mx_t^m + q\left(x_t - mx_t^m\right)\right)}{x_t\,(\varepsilon s + x_t q A_{11}(\lambda + N_t s) + A_{11}(\lambda + N_t s)x_t^m(1-q))} \right) & \text{if } z = 1; \text{ otherwise} \\[2em] x_t + vx_t(1-x_t)\left(\dfrac{-\lambda A_{12}\left(m(1-x_t)^m + q(1-x_t - m(1-x_t)^m)\right)}{(1-x_t)\,(\varepsilon s + (1-x_t)q A_{12}(\lambda + N_t s) + A_{12}(\lambda + N_t s)(1-x_t)^m(1-q))} \right) \end{cases}$$

(4b)

very small). The population size remains constant when $\varepsilon = 0$ because the recruitment rate is then always the maximum possible; even then, x exhibits small fluctuations around 1/2 as different year types select for higher or lower values of x. Greater values of A or λ, smaller values of ε, and s close to one or zero all reduce the left hand side of condition (3), and this expands the range of trade-off shapes allowing persistence of the generalist state. In traditional lottery models, the maximum birth rate is often assumed to be the number of sites opened by the death of adults. Under this interpretation, λ is proportional to $(1 - s)$; the left-hand side of inequality (3) is then a linearly increasing function of survival

If there is a second species, both x and N need species-specific subscripts. (The trade-off parameters q and m may also differ between species, but this possibility will be ignored for simplicity.) The denominators of the right-hand sides of the above equations must then be modified by terms reflecting the consumption by species 2. (These are $N_{2t}A_{21}(q_2x_2 + (1 - q_2)x_2^m)$ in environment 1, and $N_{2t}A_{22}(q_2(1 - x_2) + (1 - q_2)(1 - x_2)^m)$ in environment 2.) The 2-species model can be used to investigate the outcome of evolution if the two types have identical parameter values and slightly differing initial trait values. This corresponds to branching (Geritz et al. 1998) in models with asexual

reproduction and mutation-limited evolution. Additional species may be added to examine the possibility of secondary branching. (Abrams (2006a,b) provides examples of this approach for a different model.) Two-species systems are explored in the following section.

Most of the analysis of equation (4) is presented in Appendix S1; it is largely based on deterministic approximations that assume low temporal variation of the variables or strict alternation of year types. Attractors in the latter deterministic systems, which are stable points or period-2 cycles, usually correspond, in the stochastic system, to distributions that remain in the vicinity of these deterministic attractors for relatively long periods. We will also refer to such states in the stochastic system as attractors, although evolution away from a deterministic attractor may occur with a long run of one type of year in the stochastic system. We consider three potential attractors for this symmetrical system: the generalist (x varies around 1/2) and two specialists ($x = 0$ or 1). Numerical analysis is used to explore the exact dynamics of stochastic systems for particular parameter values. We begin by considering a representative system with a symmetrical trade-off, high survival, and a low half-saturation constant ($\lambda = 3$; $s = 0.85$; $\varepsilon = 1$; $A_{11} = A_{12} = 1$). This baseline example has a power-law trade-off ($q = 0$) and moderate rate of evolutionary change ($v = 0.02$). The analysis concentrates on the role of the exponent m in determining evolutionary outcomes.

Appendix S1 shows that the specialist states of this baseline system are locally unstable and the generalist is stable if $m < 1$. The deterministic approximation implies that the generalist attractor loses local stability when inequality (3) is violated ($m > 2.9586$). The specialist states are locally stable for values of m that are sufficiently close to 1. However, m values close enough to 1 produce specialist attractors having very small domains of attraction in this model; the initial x must be extremely close to the boundary value of 0 or 1 for evolution back to the boundary value (see eq. A-10). These two conditions suggest that, for $m < 1.1$, the generalist is the only attractor; for $1.1 < m < 2.96$, all three states of the system will be local attractors, while for $m > 2.96$, only the two specialists are local attractors. When there are three possible attractors the domains of attraction of the specialist states increase and that of the generalist decreases as m becomes larger.

The difference between deterministic and stochastic systems may be examined by numerical iteration of the stochastic system. An important effect of stochasticity is its potential for shifting the state of the system between the domains of attraction of different states. Figure 2 shows the numerically determined population and trait dynamics for a single species when $m = 2.8$, given initial conditions at the intermediate equilibrium point ($x = 0.5$ and $N = 13.0356$) and $v = 0.02$. This exponent is slightly below the maximum for local stability of the deterministic system. In

A Population density, *N*

B Trait, *x*
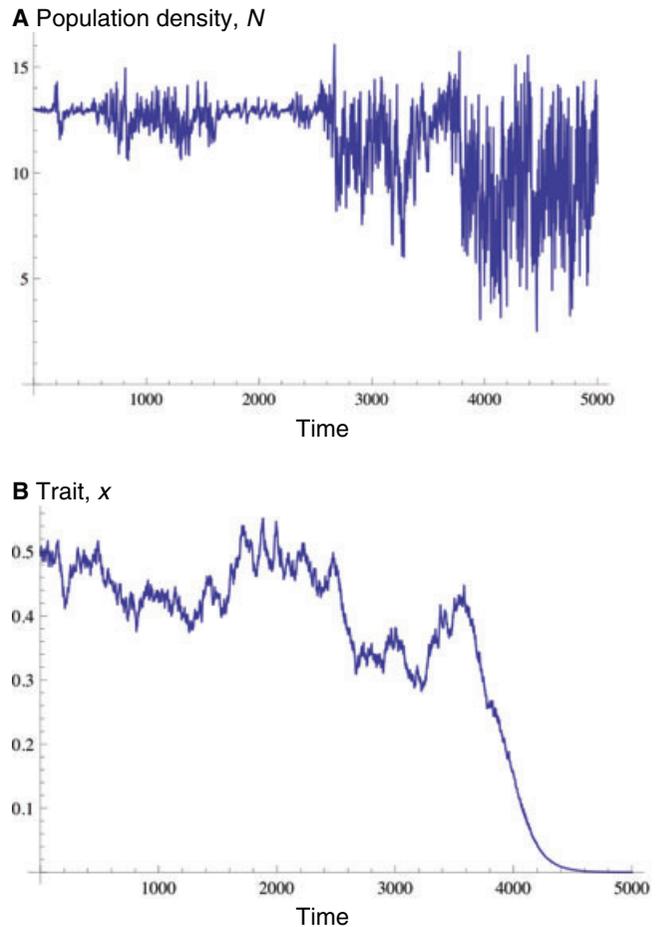
Figure 2. Evolution of a single species in an example with a strict power-law trade-off ($q = 0$), having $m = 2.8$, which is near the upper end of the predicted range of local stability of the generalist equilibrium. Other parameters are: $\varepsilon = 1$; $s = 0.85$; $\lambda = 3$; $v = 0.02$; $A_{11} = 1$; $A_{12} = 1$.

the stochastic simulation shown, x fluctuates around 0.5 until a succession of type 2 years brings the system into the domain of attraction of $x = 1$ at approximately year 4000. The variability in population size increases after specialization because of the low performance (zero reproduction) in type 2 years. This variation also contributes to a reduction in the mean population size, from approximately 13.0 in years before the transition, to 8.8 afterwards. This decrease occurs in spite of an increase of $f(x_1)$, from 0.1436 to 1.0, following specialization. The decrease in mean population size with greater variability is a consequence of Jensen's Inequality (Ruel and Ayers 1999), given that per capita growth rate is a saturating function of population size. Generalists did not transition to specialist states in simulations of 200,000 time units for any simulation of the model with the baseline parameters when $m < 2.6$. While 2.6 is more than 10% below the deterministic maximum m, the range of exponents for which $x = 1/2$ is attractive depends on v. Simulations of much longer duration with

$v = 0.001$, remained at the generalist attractor for exponents up to $m = 2.9$. Overall, equation (A-10) performed quite well in predicting the domain of attraction of the specialist state for values of m close to 1. Critical exponents based on equation (A-10) differed by less that 5% from those based on stochastic simulations, and this was not sensitive to v. If present, temporal autocorrelation of environmental states would increase transitions between states and reduce the maximum m.

The preceding example assumed a power-law trade-off. The presence of a linear term ($q > 0$) increases the range of exponents that yield a generalist, and reduces the prevalence of alternative specialist or generalist outcomes. The binomial expression for $f(x)$ also leads to some novel dynamics in the single-species system. The two specialist and the generalist states may all be unstable; parameters where this occurs are shown for the baseline system in Figure 3A, which identifies four classes of dynamics as a function of m and q. Domain 3 of the figure exhibits a pair of attractors with semispecialized phenotypes. Such outcomes were relatively common when the half-saturation value ε was small relative to the product of competitive ability and population size, linear trade-off terms were large ($q >> 0$), and the exponent m was significantly greater than 1. In the stochastic system with a moderate or large v, shifts between the two semispecialized attractors were common. Figure 3B provides an example of such shifts for a model with the baseline values of s, A_{1j}, and ε, combined with $m = 3.5$, $q = 0.3$, and $v = 0.05$. Larger values of v produce more frequent shifts between attractors and/or shifts over a wider range of exponents. Sufficiently high m ($m > 4.8$ in this case) leads to alternative specialist outcomes with x very close to 1 or to 0 and no transitions, whereas exponents less than approximately 3.2 only have a generalist attractor (see Fig. 3A).

If a single species has unequal exploitation abilities ($A_{11} \neq A_{12}$), it will often still evolve to an intermediate phenotype; the mean x is $> 1/2$ if $A_{11} > A_{12}$, and $< 1/2$ under the reverse inequality. The mean x for the generalist attractor is close to 0.5 when $A_{max}\lambda/\varepsilon$ is large ($>> 1$). However, specialization or near-specialization, even with some weak trade-offs, occurs when $A_{max}\lambda/\varepsilon$ is relatively small. The range of trade-off exponents that allow the generalist (i.e., intermediate x) attractor to be locally stable is smaller than in the symmetric case. If the baseline example is changed so $A_{11} = 1.5$ and $A_{12} = 0.5$, the generalist attractor in the stochastic system has a mean x of approximately 0.535 when $m = 1.2$, and a mean x of approximately 0.64 when $m = 2.0$. Alternative specialist and generalist attractors exist for approximately $1.11 < m < 2.05$, although the resource 2 specialist has a smaller domain of attraction. Exponents of 2.05 and greater produce specialization on resource 1 if they are started from a generalist state.

Overall, the stochastic simulations confirm the general conclusions from the analytic results in Appendix S1. A generalist is

A
Limiting exponent, m, for stability

B
Trait, x
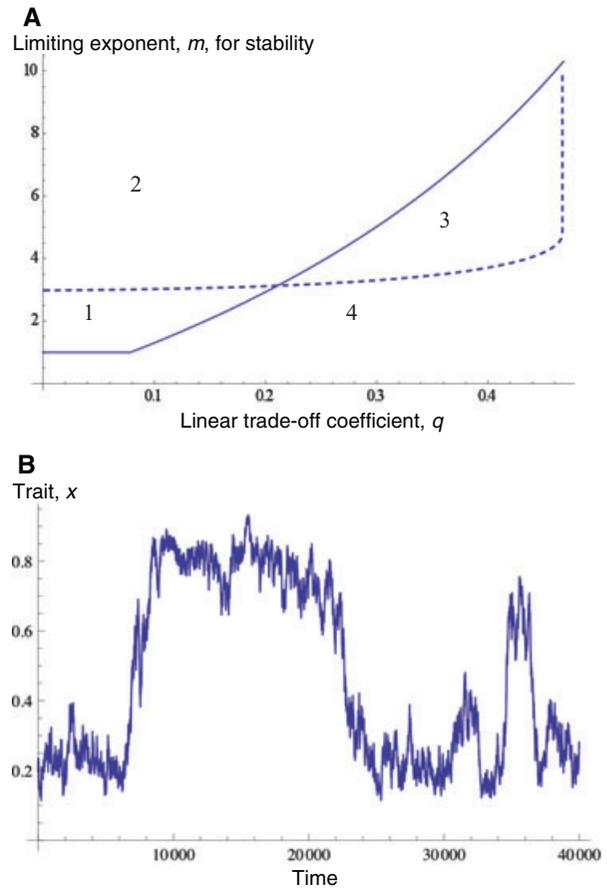
Figure 3. (A) The analytically determined bounds on stability of generalist and specialist equilibria for a symmetrical system having baseline parameters $A = 1$, $\lambda = 3$; $s = 0.85$, and $\varepsilon = 1$. The generalist state at $x = 1/2$ is locally attracting for q and m values below the dashed line, while the specialist states (0, 1) are locally attracting for parameter combinations above the solid line. Thus, zones 1 through 4 are defined as follows: 1—generalist and specialist locally attracting; 2—generalist repelling and specialists attracting; 3—generalist and specialist states repelling; 4—generalist attracting and specialists repelling. In zone 4 there are two semispecialized attracting states, one $> 1/2$ and the other $< 1/2$. The upper values of the axes are as shown because the generalist is always locally attracting for $q > 0.46781$, and exponents $m > 10$ seem biologically unlikely. Coefficients q that are close to or lower than the sharp corner in the solid line at $q = 0.078626$ produce very small domains of attraction, so the effective m for specialist stability in a finite population is somewhat higher than the solid line. (B) Temporal evolution of a trait that jumps between two semispecialized traits in a system with a strong trade-off having a significant linear component. The parameters are as in panel A with $m = 3.5$, $q = 0.3$, and $v = 0.05$.

the only outcome for large q, and it is also the only outcome at sufficiently low m when q is low to moderate. Either specialist, but not the generalist evolves at sufficiently high m, provided that q does not exceed a threshold value. A set of alternative states

(either two semi-specialist states, or the generalist and both specialist states) exist for a range of intermediate m values, again provided q is not too large.

COMPETITION AND EVOLUTION IN SYSTEMS WITH TWO (OR MORE) SPECIES

Initially identical species

Storage evolves when evolution increases a species' expected per capita growth rate when it is rare. Sympatric divergence in the relative performance in different year types has this effect, because it reduces the other species' expected competitive effect in years that are good for the focal species, particularly when the focal species is rare. The first examples in this section illustrate different scenarios under which a storage effect may evolve or increase in magnitude when two species have identical parameters and initially small differences in trait values. We later address the same question for species that initially differ in one or more parameters. In both cases, we measure the magnitude of the storage effect as the geometric mean growth rate of a rare species over a long series of years when the resident species is at its stochastic attractor.

Appendix S1 gives the conditions necessary for branching to occur at a generalist equilibrium in a symmetrical system, based on an analytical approximation assuming slow evolution (small v). We use "branching" to mean that adding a second species with identical parameter values and an initial trait value slightly different from that of the first species causes the trait values of the two species to diverge (eq. A-4), usually to more specialized states. This corresponds to situations in which a generalist state is an attractor in a 1-species model but selection is disruptive at the generalist attractor (Geritz et al. 1998). Under the dynamics given by equation (2), this leads to divergence in a 2-species model when both species have the same parameters, and both initially have very similar x values on that attractor. For example, with a pure power function trade-off and A_{ij} equal or all i, j, the branching criterion is $m > 1/s$. Both species converge to the generalist state when $m < 1/s$, but their coexistence is neutral, and extinction of one or the other in a stochastic system is inevitable. The binomial trade-off function is discussed below. For any trade-off function, population fluctuations increase in each species as its level of specialization increases during divergence.

The end point of divergence from $x = 1/2$ when $f(0) = 0$ is two specialists. This is an extreme form of storage in that the invasion fitness goes from an initial value of $W = 1$ (because the two species are initially identical) to the maximum allopatric fitness (because opposite specialists do not compete). This represents complete divergence in the temporal niches of the two species. Complete divergence in a symmetrical system occurs when the second derivative of f is large enough in magnitude (expression A-4). This expression can be used to determine the minimum m required for branching in systems with the binomial trade-off

function. The coefficient (q) of the linear terms in a binomial trade-off function affects the branching criterion in a complicated manner. As noted above, the minimum m required for branching is $1/s$ for a power function trade-off. There is a modest increase in the minimum m for branching with increasing q until q approaches 1; q close to 1 implies a near linear trade-off, and eliminates the possibility of branching. In the example considered above ($\lambda = 3$; $s = 0.85$; $\varepsilon = 1$; $A_{ij} = 1$, $v = 0.02$), divergence to specialized types is first observed for m between 1.2 and 1.25 when $q = 0.3$, and between $m = 1.3$ and 1.35 when $q = 0.5$. This compares to $m \cong 1.18$ when $q = 0$. Branching does not occur for any m when $q > 0.89$ for these parameters. If the two species have relatively high q and m values, each one in allopatry may have two semispecialized alternative attractors, as shown in Figure 3. The theory based on the universally present equilibrium points at $x = 1$, 1/2, or 0 does not apply to these semispecialized attractors, but simulations for a wide range of parameters within zone 3 in Figure 3A have all exhibited divergence to opposite complete specialization.

With asymmetric exploitation ($A_{i1} \neq A_{i2}$), it is more difficult to satisfy the branching criterion because of the lower range of exponents over which the generalist phenotype is an attractor. For example, with $q = 0$, $A_{i1} = 1.5$, and $A_{i2} = 0.5$ (and other parameters at baseline values) divergence of two species from generalist starting conditions in both species occurs for approximately $1.22 < m < 2.05$. However, even species with much stronger asymmetries exhibit divergence for a significant range of intermediate trade-off exponents when half saturation of the recruitment function, ε, is sufficiently low.

Initially different species

Here we consider two cases; in the first, only one species is capable of significant adaptive evolution in its environmental performance. In the second, both species evolve and both have trade-offs characterized by different maximum competitive abilities (A_{ij}). In both cases, each species is initially located on its allopatric generalist attractor.

The combination of one evolving and one nonevolving species led to evolution of the storage effect in Snyder and Adler's (2011) model. It is also of interest because it illustrates the pure effects of evolution in a single species, without the complications of coevolution. Introducing a fixed ($x = 1/2$) generalist with A_{ij} and m values identical to those of the evolving species causes the latter to become a specialist if it satisfies the branching criterion. However, if the generalist state is globally stable in a single-species system, the evolutionarily flexible generalist species does not evolve away from $x = 1/2$, but is at a disadvantage relative to the fixed generalist species that shares the same trade-off. The flexible species is then slowly excluded. Because of the random sequence of year types, the evolutionary response to a year of type i is equally likely to be advantageous or disadvantageous in

Mean Size of Fixed (solid) and Evolving (dashed) Populations
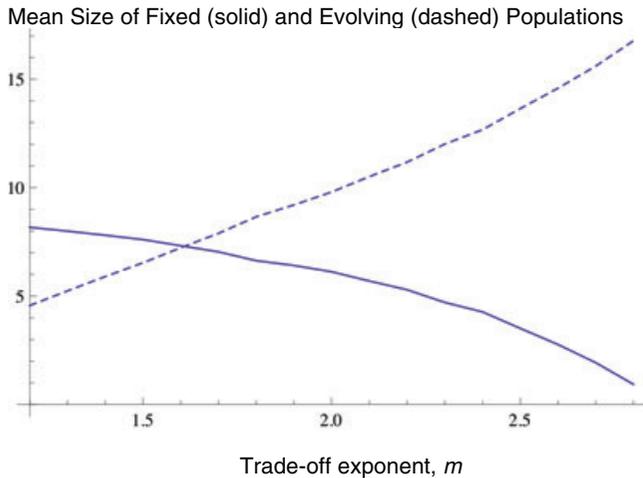
Figure 4. Mean population sizes of sympatric generalist (solid—species 1) and specialist (dashed—species 2), as a function of the trade-off exponent, m. This is applicable to either a system with two inflexible species or an evolving species (that becomes specialized on resource 2, so $x_2 = 0$) versus a fixed generalist. Higher exponents make the generalist progressively less efficient due to a lower attack rate. The other parameter values are: $\varepsilon = 1$; $s = 0.85$; $\lambda = 3$; $q = 0.3$, $v = 0.05$; $A_{11} = 1$; $A_{12} = 1$; $A_{22} = 1$; $A_{21} = 1$.

the following year; the shape of the recruitment function implies that the variation reduces mean fitness, so the flexible species is excluded. One would expect selection against evolutionary flexibility (decreased v) in this scenario (Kawecki 2000).

If $m > 1/s$, the evolving and fixed generalist species are usually able to coexist because the evolving species diverges. The qualification (usually) arises because, when m is only slightly greater than the branching threshold, divergence may be slow enough that the density of the evolving species drops to levels that would ensure exclusion in most finite populations before divergence allows it to increase. When coexistence occurs, the final competitive impact of the fixed generalist on the evolving species is larger when m is smaller. If m is relatively large, the generalist has lower competitive abilities ($f(1/2) \ll 1/2$), and therefore fares worse in competition with the evolved specialist. Figure 4 shows how the densities of the two coevolved species depend on the trade-off exponent, m. Larger values of m favor the specialist, while smaller values result in a much higher density for the fixed generalist.

A more likely scenario assumes that species initially differ in A_{ij}, or some other parameters, and both evolve in response to sympatry. When each has a generalist attractor in allopatry, both usually diverge following the sympatry. If our baseline example is changed so that $A_{11} = 1.5$ and $A_{12} = 0.5$, $A_{21} = 0.5$ and $A_{22} = 1.5$, the evolutionary equilibrium mean values of x_1, x_2, N_1, and N_2 change following invasion of species 1 by species 2 as shown in Figure 5. In a system with a single species, the mean value of x
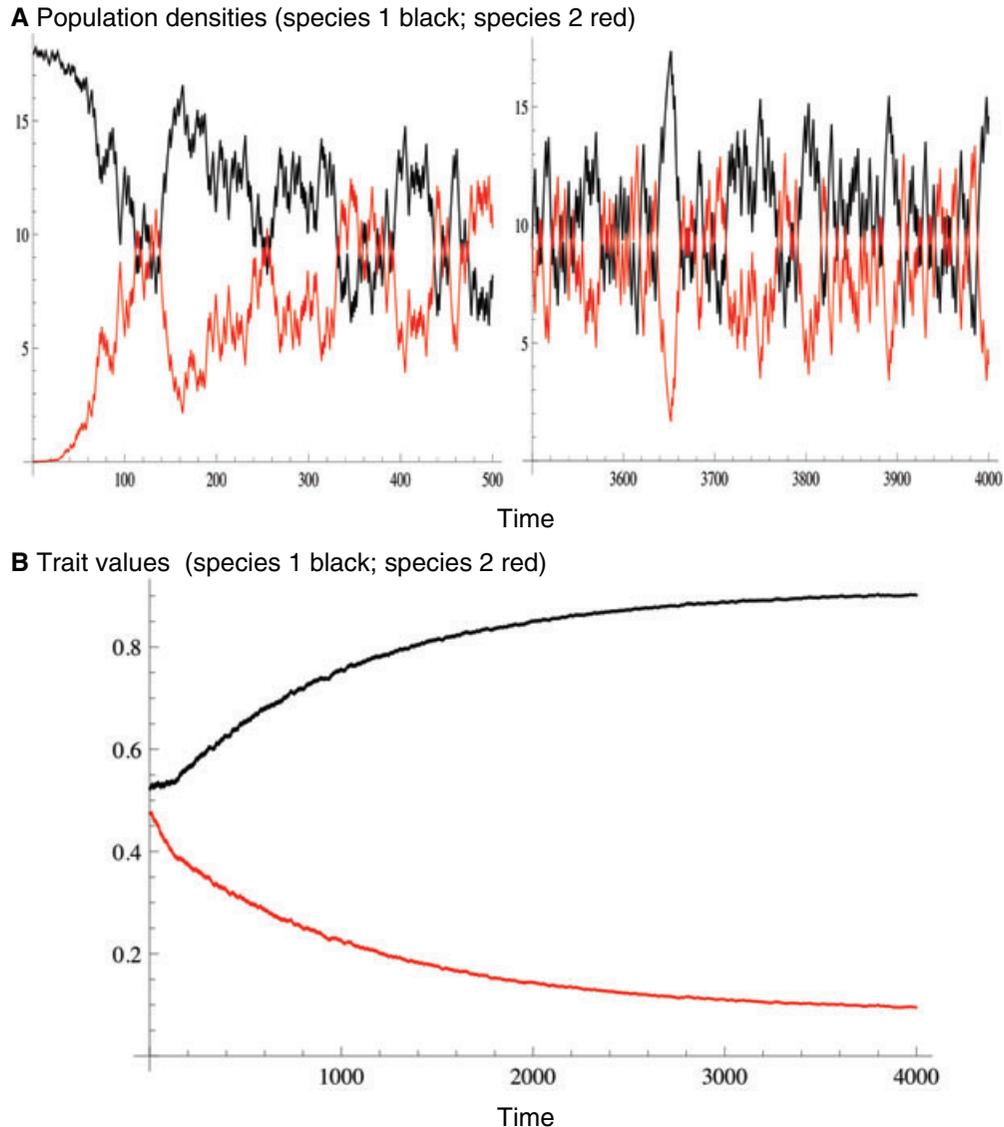
is $> 1/2$ when $A_{i1} > A_{i2}$, and $< 1/2$ when this inequality is reversed. However, the allopatric mean x is relatively close to 1/2 when ε is small relative to the total utilization rate ($\Sigma ANf(x)$). The example in Figure 5 has a threefold difference in a species' A values, and a total utilization close to 20 times ε; this yields an allopatric mean trait of $x_1 = 0.524$ for species 1 and $x_2 = 0.476$ for species 2. The displacement in sympatry causes divergence to $x_1 = 0.916$ and $x_2 = 0.084$, implying considerable temporal resource partitioning (i.e., a storage effect). The magnitude may be measured by the change in the invasion fitness of species 2 caused by this displacement. For Figure 5, that advantage is a geometric mean invader growth rate of 1.3934 after divergence, compared to 1.0820 for one species' allopatric phenotype invading the allopatric form of the other species. Figure 5 shows that the initial divergence of the rare invader (species 2) is quite rapid. As divergence proceeds, divergence slows and the periods of dominance of one species shorten.

The magnitude of the displacement in sympatry becomes larger when the initial difference in maximum attack rates, $|A_{i1} - A_{i2}|$, is larger, given the mirror-image symmetry in attack rates assumed here. Larger trade-off exponents within the range of weak ($m < 1$) trade-offs also imply a greater shift in sympatry; increasing m from 0.5 to 1 in the example from Figure 5 yields complete specialists in sympatry, even though the allopatric mean trait values differ only slightly ($x = 0.532$ and 0.468 for species 1 and 2, respectively) from those in the otherwise-comparable system with $m = 0.5$. When the A values for different environments differ, larger half-saturation constants (ε) favor evolution of a greater degree of specialization, both in allopatry and sympatry. However, changing ε often causes a relatively small change in the magnitude of divergence, because both allopatric and sympatric trait values are changed in the same direction.

Mirror-image symmetry in competitive abilities in the two environments is not required for character divergence in this scenario with different, weak trade-offs. However, divergence is usually asymmetrical. Assume species 1 and 2 have the same mean A_{ij}, but have different ratios of A_{1j}/A_{2j}. If, for both species, $A_{1j} > A_{2j}$, and there is coexistence following sympatry, the species with a higher ratio becomes more specialized on environment 1, exhibits a larger shift in its trait, decreases in abundance, and becomes more variable following divergence.

Evolution of two species when other mechanisms allow coexistence

In the above examples, temporal partitioning of resources via between-year differences in competitive performance was required for coexistence. Previous work on resource partitioning based on resource identity has revealed that parallel displacement, usually involving a net convergence or divergence of traits, frequently occurs when some resources or factors unrelated to the

A Population densities (species 1 black; species 2 red)

Time

B Trait values (species 1 black; species 2 red)

Time

Figure 5. Character displacement of two species with different sets of maximum utilization rates. Parameter values common to both species are: $m = 0.5$; $\varepsilon = 1$; $s = 0.85$; $\lambda = 3$; $q = 0.3$, $v = 0.02$. Species 1 has $A_{11} = 1.5$ and $A_{12} = 0.5$, while species 2 has $A_{21} = 0.5$ and $A_{22} = 1.5$. Species 2 is a rare invader. Both species initially have x values equal to their long-term means in allopatry (0.524 for species 1 and 0.476 for species 2). The initial population of species 1 is also at its allopatric mean (17.95). The population is only shown for the first and last 500 years of 4000.

evolving trait allow coexistence in the absence of partitioning of the trait-related resources (Abrams 1986, 1987a). In our 2-species models, additional limiting factors could allow coexistence without the storage effect. We have investigated two models with such factors; in one, there is purely intraspecific density dependence in survival; $s_i = s_{0i}/(1 + \beta_i N_i)$, where s_{0i} is the maximum survival probability and β_i measures the strength of the density dependence. In the second model, resource partitioning within a year is implemented by weighting N_i by a competition coefficient, α in the dynamical equations for species j, and vice versa. If $\beta > 0$ in model 1 or $\alpha < 1$ in model 2, coexistence is possible without any difference between environmental performance traits. How-

ever, divergence of x values still occurs in sympatry for the vast majority of systems, and this leads to or increases the storage effect. Parallel change occurs for otherwise very similar species with density-dependent survival. Detailed results for these models will be presented elsewhere (P. A. Abrams et al., unpubl. ms.).

Evolution with more species and more environmental states

The main model considered above has only two competing species and two environmental states. However, the general circumstances when evolution of a storage effect is expected do not depend on

these assumptions. It is easy to confirm that having a third resource whose utilization is independent of the trait does not qualitatively alter the expectation of divergence in use of the original two resources. We have examined analogous models having a continuous range of states characterized by a continuous environmental variable. The consumer species are characterized by unimodal "environment utilization curves," describing their competitive ability, A, as a function of the environmental variable. We assumed utilization curves have a fixed form and evolve by shifts in their position, with negative effects on other fitness components when that position is suboptimal. Evolutionarily stable utilization curve positions were determined using methods similar to those employed above. The traits of two species (utilization curve positions) diverge in such cases, producing or enhancing a storage effect (P. A. Abrams et al., unpubl. data).

Discussion

Our introduction highlighted the puzzling fact that two previous studies have concluded that evolution did not produce or enhance coexistence via the storage effect. Nevertheless, the existence of this mechanism has been supported by empirical work. Our analysis of simple models shows that coexistence, or more robust coexistence, via the storage effect is expected to evolve under lottery competition for a wide range of conditions. Further, such evolution occurs under circumstances that are analogous to those that allow coexistence to evolve via nontemporal resource partitioning. Indeed, we found that increased temporal partitioning can result from evolutionary branching within a single, relatively homogeneous species (lineage), or from character divergence of species that initially differ in their trade-off relationships. These results suggest that, given environmental variability affecting recruitment and a related trade-off in traits, the storage effect often evolves, producing and/or maintaining diversity.

This conclusion differs from that recently reached by Snyder and Adler (2011), and from earlier work by Kisdi and Meszéna (1995). Although there are minor differences between the population dynamics given by equation (1) and those described by these previous models, the primary difference lies in the type of trait that is assumed to evolve. Because the "storage effect" mechanism consists of several components, it is possible for traits affecting different components to be affected differently. The work by Kisdi and Meszéna (1995) failed to find a positive effect of coevolution on coexistence in a local context; evolution of a trait determining position on a trade-off between survival and reproductive rate produced priority effects in their model. Such trade-offs are likely to occur in some systems, and it would be interesting to explore the interaction of this type of trait with those that determine the relative competitive abilities in different environments. Similar fecundity-survival trade-offs in a simple nonlottery system were

shown to have potentially positive or negative effects on coexistence (Abrams 1987a).

Snyder and Adler (2011) based their model on annual plants with a seed bank and assumed that variation in the germination fraction is the evolving parameter. Because variability per se is disadvantageous, and because the seed stage was not the competitive stage, they found that variability would generally decrease, so that the storage mechanism would usually tend to disappear. However, they also found that storage could evolve if the germination rate was positively correlated with performance in the subsequent competitive seedling stage. While this "predictive germination" was treated as a special case, it seems likely as a product of adaptively evolving germination cues (Pake and Venable 1996; Angert et al. 2009). Performance during the competitive stage of most systems will depend on some traits that involve a trade-off in performance between different year types. Evolution in this scenario causes resource partitioning to increase. Evolution of the storage effect is then simply evolution of temporal resource partitioning, and it can produce evolutionary branching and/or character divergence under circumstances similar to those for analogous models of nontemporal partitioning.

This similarity is reflected in previous evolutionary models of competition based on resource partitioning in deterministic environments. Rueffler et al. (2006) analyzed the evolution of resource partitioning between two consumer species using such a model with abiotic resource dynamics, where the within-year expressions for birth and survival were very similar to those used here. They assumed a power-law function for the trade-off in resource utilization rates, and found that branching occurred when the trade-off was strong and the generalist equilibrium was stable. The difference in the form of the models of Rueffler et al. (2006) and those considered here arises from temporal segregation in our models, which leads to a multiplicative rather than an additive combination of fitness contributions from different resources. The multiplicative form means that stronger trade-offs are required for divergence of initially similar species. This analogy to traditional character displacement suggests that sympatric-allopatric trait comparisons are likely to be a productive approach to identifying potential examples of the evolution of storage. Another similarity of our storage models and traditional resource-partitioning models of character displacement is that adaptive specialization of one species often decreases its population size (Abrams 2012).

The model considered here also has many similarities to previous continuous time models of the evolution of specialist and generalist types in environments where there are two spatially or physically distinct resources (Egas et al. 2004; Abrams 2006a,b; Ravigne et al. 2009). Although there are no physical differences between the resources present in different years in our models, years are dynamically independent; consumption (recruitment) in one year does not affect resource abundance or opportunity for

recruitment in the next. This makes them effectively distinct resources for the purpose of coexistence (Haigh and Maynard Smith 1972; Abrams 1988). However, the complete temporal segregation of the two "resources" in our model changes the form of the fitness function, changing the conditions for the evolution of specialists and generalists from those in models with nontemporal partitioning.

Literature on the storage effect has concentrated on systems with stochastic variation. However, the ecological and evolutionary consequences of competition can be very similar when there is regular alternation of resources or environments, and consumers experience a trade-off in their abilities to use the different environments. In fact, some of our approximate analytical results are based on a fitness expression that is an exact model for such seasonal alternation. Storage effect models also usually represent systems in which different life stages have different limiting factors. However, resource partitioning via different temporal patterns of resource consumption also allows coexistence in systems lacking population structure (Abrams 1984). In such systems evolution favors increased partitioning under circumstances qualitatively similar to those described here.

We did not explicitly consider the ability of evolution to allow coexistence of two species whose initial traits would lead to deterministic exclusion of one by the other. This outcome is possible given a large enough population of the inferior species and sufficiently rapid evolution. It is especially likely in a metacommunity context with spatial variation in competitive dominance, where some patches allow the on-average inferior competitor to coexist in the absence of evolution. However, these considerations are identical for traditional character displacement due to nontemporal resource partitioning; here too, evolution of the ability to coexist from a state of deterministic exclusion in a homogeneous system depends on the inferior competitor's initial population size being large enough and its rate of evolution being sufficiently rapid.

Our analysis is limited in that we do not examine the long-term stochastic distribution of trait values, and our main model assumes a very simple form of environmental variation (two states; no autocorrelation). Equation (2) assumes a simple and extreme form for the change in genetic variance with mean trait value that makes the specialist phenotypes into absorbing states because genetic variance disappears completely at those states. We have briefly mentioned unpublished work on models with more states and others with mechanisms that prevent variation from disappearing in specialists; preliminary analyses of these (P. A. Abrams, unpubl. data) have yielded results broadly similar to those described here over ecologically relevant time scales. Learning more details of the impact of ecological factors on the temporal distribution of trait values is an important area for future work, as are studies using more realistic genetic models.

We end by considering empirical evidence regarding both the assumptions and the predictions of the model. Our model requires a trade-off in performance for different types of years. Such a trade-off should arise for the same reason that performance on physically different resources or in different habitat patches evolves: different traits are often required for optimal performance in qualitatively different conditions. Many species that experience temporal environmental variation show evidence of such trade-offs. For example, the relative success of groundfish spawning has been shown to depend on environmental conditions, with different species favored in different years (Brodziak and O'Brien 2005). For fish species with sedentary adults and dispersing larvae, variation in spawner-recruitment relationships is generally assumed to be a consequence of unknown or unmeasured environmental factors. Plant species similarly show great temporal variation in recruitment, probably because of abiotic variation (Warner and Chesson 1985; Facelli et al. 2005). The evolution of different sets of environmental sensitivities is likely to be common.

Although few studies have examined storage effects in terms of the underlying traits, research on winter annual plants from the Sonoran desert has shown two trait axes to be important for the storage effect. These species show a trade-off between water-use efficiency and relative growth rate, which translates to a reproductive advantage in dry and wet years, respectively (Huxman et al. 2008; Kimball et al. 2012). This provides a rare-species advantage, promoting coexistence through the storage effect (Angert et al. 2009). The second axis in these desert annuals involves an increase in the seedbank with an increase in interannual variation in fecundity (Pake and Venable 1996; Venable 2007). Although this second scenario is not explored in our model, it suggests that variation in the environment may promote the conditions required for evolutionary branching (eq. A-4), further promoting evolution of the storage effect.

The scarcity of empirical evidence for character divergence of environmental sensitivities is probably due largely to the lack of previous theory suggesting that it is likely to occur. We hope that our work will stimulate such studies. If such displacement occurs, it could be a significant factor influencing geographic variation in species diversity.

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Supporting Information

The following Supporting information is available for this article:

Appendix S1. Stability of equilibria in a symmetrical system.

Supporting Information may be found in the online version of this article.

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