Environmental uncertainty, autocorrelation and the evolution of survival

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Survival is a key fitness component and the evolution of age- and stage-specific patterns in survival is a central question in evolutionary biology. In variable environments, favouring chances of survival at the expense of other fitness components could increase fitness by spreading risk across uncertain conditions, especially if environmental conditions improve in the future. Both the magnitude of environmental variation and temporal autocorrelation in the environment might therefore affect the evolution of survival patterns. Despite this, the influence of temporal autocorrelation on the evolution of survival patterns has not been addressed. Here, we use a trade-off structure which reflects the empirically inspired paradigm of acquisition and allocation of resources to investigate how the evolutionarily stable survival probability is shaped in variable, density-dependent environments. We show that temporal autocorrelation is likely to be an important aspect of environmental variability that contributes to shaping age- and stage-specific patterns of survival probabilities in nature.

Keywords: autocorrelation; ES allocation strategy; semelparous; stochasticity; survival; trade-off

1. INTRODUCTION

In uncertain environments, theory predicts that selection will favour individuals who spread their risk across years (Cole 1954; Murphy 1968; Gadgil & Bossert 1970; Bell 1974, 1980; Schaffer 1974; Orzack 1985). Many traits may contribute to risk-spreading: well-known examples include iteroparity, variable age at maturity (Wilbur & Rudolf 2006) and delayed seed germination (Cohen 1966; Rees et al. 2006). Although such traits might be maladaptive in a constant environment, their ubiquity in natural populations can be explained by the fact that they increase fitness when environments are stochastic.

Variable environments may also be autocorrelated (Halley 1996; Schwager et al. 2006), which can alter both population structure and growth (Tuljapurkar & Haridas 2006). Despite this, most work on life-history evolution in variable environments has not considered autocorrelation (but see Tuljapurkar & Wiener (2000)). The evolution of traits related to risk-spreading could be particularly affected because the autocorrelation structure of the environment contains information on what the future holds. We might therefore anticipate that autocorrelation will interact with environmental variance in determining the evolutionarily stable (ES) strategy for demographic characters related to risk-spreading, and could thus have considerable implications for life-history evolution.

If trading-off current reproduction for increased chances of survival results in no benefit to future reproduction (e.g. increased growth or future fecundity), then such a life-history decision would be maladaptive in a constant environment. However, in a variable environment, increased survival could spread offspring presence across a range of years, providing a fitness advantage by diluting risk. Wilbur & Rudolf (2006) recently showed that for certain life histories, directional selection pressures on juvenile and adult survival can increase with environmental uncertainty, leading to the prediction that longer lifespans should evolve in stochastic environments. However, the force of stabilizing selection (for example, through optimization of resource allocation) is likely to be at least as important as directional selection, but has not yet been considered for the evolution of survival trajectories in uncertain environments. Temporal autocorrelation, although likewise so far neglected, could also be important. Temporal autocorrelation conveys information about future environmental conditions and, depending on the nature of this information, selection might favour increased lifespan at the expense of reproductive output, or the opposite.

The struggle to quantify trade-offs in natural systems inspired the notion of contrasting acquisition of resources against allocation of resources when considering trait covariation. For example, survival and reproduction may show negative covariation because resources are limited and must be allocated between them (i.e. a trade-off; van Noordwijk & de Jong 1986; Benton et al. 2006), or positive covariation because variance in environmental conditions swamps patterns of limited resource allocation (van Noordwijk & de Jong 1986; Cam et al. 2002). Although environmental variation is beyond individuals’ control, resource allocation between vital rates should still be subject to strong natural selection in variable environments. For example, if adult survival is unlikely for reasons beyond individuals’ control, selection should favour individuals who invest more in reproduction at the expense of survival. The most extreme example of this is semelparous species, where reproduction is fatal. The interaction between allocation and...
acquisition of resources in determining trait values will be important for the evolution of survival trajectories because changes in acquisition of resources may interact with allocation patterns, so that the shape of the trade-off (concave or convex) can change with the environmental context. Different trade-off structures can lead to different outcomes (Takada 1995), and temporal variation in the trade-off structure is likely to be particularly important in shaping life histories in fluctuating environments (Orzack & Tuljapurkar 2001).

Semelparous species are convenient for exploring allocation between reproduction and survival, as there is no complication in accounting for costs of reproduction. For example, prior to flowering, semelparous plants should allocate resources entirely to either survival or growth (Metcalf et al. 2006), and growth leads to increased reproduction. Additionally, the life cycle of semelparous species is well known, and in particular there is information on how density dependence operates (Metcalf et al. 2003), which is recognized as being important in the evolution of risk-spreading (i.e. bet-hedging; Wilbur & Rudolf 2006).

Here, we take fecundity as a proxy for growth within a season, and use simple models to measure the long-term fitness of semelparous life histories with different patterns of resource allocation to either survival or fecundity in stochastic environments with temporal autocorrelation. We ask whether stochasticity and autocorrelation can favour increased allocation towards survival in semelparous species. To explicitly address this question, we consider a situation where there are no direct benefits of longer lifespan (e.g. higher fecundity attained by delayed maturity and enhanced growth). We then conclude by discussing our results in the context of what is known about the physiology of growth–survival trade-offs of monocarpic plants and make predictions relative to survival in different environmental contexts.

2. MATERIAL AND METHODS

(a) Models of the environment

Environmental conditions in time step $t$ were denoted by $X_n$, where increasing values of $X_n$ corresponded to increasing quality of the environment. Three situations were modelled.

(i) Constant environments

A constant environment corresponds to a situation where the environment retains the same value for all $t$. We explored the effects of constant environmental quality on the optimal resource allocation strategy (model described below) by setting $X_n$ at values ranging between $-4$ and $4$.

(ii) Stochastic environments with different levels of variability

To model stochastic environments with different levels of variability, we set the mean environment to $X_n=0$, and then generated deviates from a normal distribution with mean 0 and increasing variation to obtain sequences of environmental conditions through time, $X_{n+1}$, such that $X_{n+1} \sim N(0, \sigma_n)$, for a range of $\sigma_n$. These sequences of environmental conditions could represent, for example, rainfall, sunlight, or a range of other variables from the biotic or abiotic environment, either within or between years. To explore their impact on allocation strategies, we used sequences of $T=10$ 000 iterations and discarded the first 1000 to minimize the influence of initial conditions.

(iii) Stochastic environments with different degrees of autocorrelation

To model autocorrelated environmental conditions over time, we used an autoregressive model with a time lag of one (AR1)

$$X_{t+1} = \alpha X_t + \epsilon_{t+1},$$

where $\alpha$ is the autocorrelation parameter ($|\alpha|<1$) and $\epsilon$ is a normally distributed random variable $\epsilon \sim N(0, \sigma)$ (Schwager et al. 2006). We varied $\alpha$ between $-0.99$ and $0.99$ and normalized the resulting sequences, so that $X_0 \sim N(0, \sigma)$ with $\sigma=1$ (Wichmann et al. 2005). To explore the effects of temporal autocorrelation in the environment on the optimal resource allocation strategy, we again used sequences of $T=10$ 000 iterations and discarded the first 1000 to minimize the influence of initial conditions.

(b) Demographic models for the optimal allocation

To model population dynamics, we used a two-stage matrix model of a semelparous life history,

$$
\begin{pmatrix}
J_{t+1} \\
A_{t+1}
\end{pmatrix} =
\begin{pmatrix}
P(1-\gamma) & p_c F \\
p_c \gamma & 0
\end{pmatrix}
\begin{pmatrix}
J_t \\
A_t
\end{pmatrix}.
$$

The probability of maturing is denoted by $\gamma$; $P$ indicates the probability of survival; $F$ captures fecundity (number of offspring produced); and $p_c$ indicates the probability of offspring establishment. $F$ and $P$ are determined by allocation of resources to either fecundity or survival; and by the environmental conditions $X_t$ or $X_t=|X_1, X_2, X_3, ..., X_T|$. With $\gamma<1$, this model leads to a population with overlapping generations.

There are several possible ways to model the joint effect of resource allocation and variation in environmental conditions. Here, we assumed that individuals allocate a fixed resource base to either survival or fecundity; once this allocation decision is made, environmental variability is added to determine the overall survival or fecundity. The allocation decision and environmental conditions of the previous time step were assumed to have no direct effect on the current time step. We chose $P = (e^{\alpha_{t+1} + X_t})/(1 + e^{\alpha_{t+1} + X_t})$ to constrain survival between 0 and 1, and $F = e^{\alpha_{t+1} + X_t}$, where $X_t$ is the value of the environment at time $t$ and $\pi$ captures allocation of a single static resource pool that individuals convert into survival with efficiency defined by $c_1$, and into fecundity with efficiency $c_2$. The conversion efficiency parameters adjust for the fact that fecundity and survival are on different scales; and changes in these parameters capture how one unit of resource might lead to larger or smaller increases in survival or fecundity dependent on efficiency. We refer to a particular value of $\pi$ as a phenotypic strategy; the chosen strategy or value of $\pi$ controls the allocation of resources between survival and fecundity (i.e. the trade-off strategy). We assume that $\pi$ is under genetic control, and then evaluate the values of $\pi$ that will evolve in different scenarios.

This model structure captures systems where individuals have a starting amount of resources each year, and allocation decisions between survival and fecundity must be made, despite a lack of information about conditions through the rest of the year. It has the advantage of allowing changes in trade-off structure over time (Orzack & Tuljapurkar 2001).
Each changes capture the biological fact that in good environmental conditions, allocating resources towards survival will not greatly improve survival probability, as it will be close to its maximum value of 1. However, in poor environmental conditions, survival probability will be far from its maximum, and thus, allocation towards survival can have a large impact on survival probability (see figure 1). Changing the conversion parameters $c_1$ and $c_2$ shifts the lines of the $P$ and $F$ landscapes (figure 1); changing variance and autocorrelation shifts the pattern of how the environment moves across the landscape from left to right.

As $\pi$ is constrained between 0 and 1, the fecundity and survival landscapes have fixed boundaries, which affect the optimal allocation. In particular, if survival is too high within these boundaries, allocation towards it will never be optimal. As defined previously, survival $P$ is high in all environments for a range of $c_1$ and $c_2$. Allocation towards survival and away from fecundity is therefore never optimal. However, in natural populations, traits correlated with high survival will rapidly go to fixation, and observed variation in patterns of survival should result because different allocation strategies are optimal in different environments. We therefore diminished the relationship defining $P$ by a constant $c_3$ in all environments $P = (e^{c_1 + X_t - c_3})/(1 + e^{c_1 + X_t - c_3})$ to capture situations where intermediate allocation to survival could be optimal. To ensure that allocation strategies could significantly alter the life-history trajectory, we chose values of $c_1$ and $c_2$ such that changes in allocation were not swamped by environmental variation. We then explored the implications of different resource conversion efficiencies by altering $c_1$ and $c_2$ (figure 1).

(c) Modelling evolutionary dynamics

To model evolutionary dynamics, we assumed that density dependence acts on offspring establishment ($p_e$ in (2.2)), as is the case for many semelparous plant species (Metcalf et al. 2003). In this situation, in each year, all seeds produced in the previous year compete on an equal footing for a limited number of microsites which will allow establishment. We assumed that the environment was saturated with seeds, so that all microsites are occupied in each year. We then considered the population growth rate of an invading phenotype into an environment set by a chosen resident strategy in a context determined by either a static environmental value $X$ (constant environment), or a stochastic environmental sequence $X_t$ or $X_s$. The resident affects the invader only through density dependence acting on offspring establishment (we assume that the invader’s effect on itself and the resident is negligible because it invades from low densities; Metz et al. 1992). The probability of establishment for the invader’s offspring in each time step is therefore determined by the number of offspring produced by the resident in the previous time step. The invader’s survival $P$ and fecundity $F$ are determined by its strategy $\pi$, and the environmental value $X$ or $X_t$.

(i) Constant environments

Mylius & Diekmann (1995) have shown that in this density-dependent context, the constant environment ES allocation strategy corresponds to that which maximizes $R_0$. We therefore estimated $R_0$ for all allocation strategies $\pi$ for a range of values of $X_t$ between $-4$ and $4$. The value of $\pi$ corresponding to the maximal $R_0$ identifies the constant environment ES $\pi$ for that $X_t$, denoted by $\pi_X$.

(ii) Stochastic environments

In a stochastic environment, evolutionary dynamics is regulated by the stochastic growth rate $\vartheta$ of an invader into an environment determined by the resident strategy $\pi$, in a context defined by environmental conditions over time $X_t$ or $X_s$ (Metz et al. 1992). To establish the resident’s dynamics, we iterated (2.2) by calculating $P$ and $F$ corresponding to $X_t$ at each time step and the resident’s strategy $\pi$. From this, we calculated the probability of establishment for offspring produced in each time step, assuming that this was determined by a constant number of microsites available in the following time step:

$$p_e(\vartheta) = \frac{M_{t+1}}{A_{t+1}e^{1-\pi_X}}$$

where the subscript $t$ denotes the resident; $M_{t+1}$ is the number of microsites available in time step $t+1$, taken as a constant value of 10 (altering this value does not change outcomes); and $A_{t+1}$ is the number of resident adults in time step $t$. The denominator in (2.3) is therefore the total number.

Figure 1. (a) Landscape of survival probability, $P = (e^{c_1 + X_t - c_3})/(1 + e^{c_1 + X_t - c_3})$ (see text) across the range of possible allocation conditions $\pi$ and environmental conditions $X_t$, taken with $c_1 = 8$ and $c_2 = 5$. Decreasing $c_1$ decreases the slope of the landscape in the plane of $\pi$. Decreasing $c_1$ shifts the landscape to the right. (b) Landscape of fecundity $F = e^{X_t + 3}$ with $c_2 = 6$. Decreasing $c_2$ decreases the slope in the plane of $\pi$. For both $F$ and $P$, increasing the variance will extend the width of these landscapes, with more extreme values of $X_t$ on the left and right. For high positive autocorrelation, the environment will spend more consecutive time only on the left or only on the right. For high negative autocorrelation, the environment will move sequentially from the left side to the right. (c) Resulting trade-off between fecundity (log scale) and survival in different environmental conditions. Moving from left to right along the curves corresponds to increasing values of $\pi$ for the worst environment, $X_t$ (represented by a solid line), mean environment (dotted line) and best environment (dashed line).
We calculated and stored the resulting \( p \), where

\[
T = Z_g \frac{A_i + A_e}{2}
\]

By iterating (2.4) over time, the invader’s rate of invasion incorporating (2.3) into (2.2), we obtain the matrix and strategies (Geritz et al. 1992).

To obtain the ES resource allocation strategy in a stochastic environment, we chose a resident strategy and ran it through the \( T \) time steps of environments \( X_t \) or \( X_{t+1} \), where \( T \) is sufficiently large to approximate dynamics at \( \infty \). We calculated and stored the resulting \( p_{es}(t) \) at every time step following (2.3). We then invaded this resident by a range of invading strategies \( (0 \leq \pi \leq 1) \), whose dynamics were defined by \( X_t \) or \( X_{t+1} \), \( p_{es}(0) \), which is equal to \( p_{es}(t) \) in (2.3), and (2.4). If \( \theta \leq 0 \) the invasion fails; otherwise, the invading phenotype can successfully establish itself in the population. Once we identified a strategy that could successfully invade, we set this as the new resident strategy.

To test implications of our modelled trade-off structure, we re-ran the analyses with additive rather than multiplicative effects of resource allocation to fecundity, i.e. \( F = (1 - \pi) c_2 + X_t \). Qualitative results were identical except that no value of \( c_2 \) led to decreases in ES allocation to survival with increasing variance in environmental conditions.

3. RESULTS

(a) ES allocation strategies

To predict when allocation to survival at the expense of fecundity should occur, we calculated the ES values of \( \pi \) with \( c_1 = 8 \), \( c_2 = 6 \) and \( c_3 = 5 \) for (i) constant environments with different static values of environmental quality, (ii) stochastic environments with increasing levels of variation, and (iii) stochastic environments with increasing levels of autocorrelation, exploring for each case sensitivity to conversion parameters and the maturation rate.

(i) Constant environments

In a constant environment, as the environment’s quality \( X_t \) increased, the ES allocation of resources towards survival decreased, and fecundity was favoured (figure 2a). If \( c_1 \) or \( c_2 \) were lower, the qualitative pattern remained the same, but higher environmental quality was required for an equivalent allocation towards fertility. Allocation towards survival was never optimal when \( c_3 \) was sufficiently high, or \( c_1 \) sufficiently low.

(ii) Stochastic environments with different levels of variability

In a stochastic environment, as the environment became more variable, ES allocation to survival decreased (figure 2b). If maturation was more likely (i.e. \( \gamma \) higher), less resource allocation to survival evolved for any given level of variability. This occurred because, as individuals matured faster, they spent less time at risk in the juvenile stage.

Across a range of \( c_1 \) values, the qualitative relationship between ES allocation to survival and the level of environmental variation (figure 2b) was retained; higher \( c_1 \) values led to higher ES allocation towards survival (not shown). However, the qualitative pattern was insensitive to values of \( c_2 \). For low \( c_2 \), allocation towards survival increased as the environment became more variable, whereas for high \( c_2 \), allocation towards survival decreased (figure 3a).

To test implications of our modelled trade-off structure, we re-ran the analyses with additive rather than multiplicative effects of resource allocation to fecundity, i.e. \( F = (1 - \pi) c_2 + X_t \). Qualitative results were identical except that no value of \( c_2 \) led to decreases in ES allocation to survival with increasing variance in environmental conditions.

(b) ES allocation \( \pi^* \) in a constant environment for \( \gamma = 0.6 \) (solid line), \( \gamma = 0.8 \) (dashed line) and \( \gamma = 0.99 \) (dotted line), with \( c_1 = 8 \), \( c_2 = 6 \) and \( c_3 = 5 \). (b) ES allocation towards survival \( \pi^* \) in stochastic environments with increasing variance \( \sigma^2 \), line types are the same as given in (a). (c) ES allocation strategy \( \pi^* \) in stochastic environments defined by different \( \alpha \) values for the same overall variance, \( \sigma^2 = 1 \). When \( \alpha < -0.5 \), there is no stable ES allocation strategy for each value of \( \gamma \). Although strategies on the lower line can invade all others, they can be invaded by strategies in the area between the lower and the upper lines.

Figure 2. (a) ES allocation towards survival \( \pi^*_g \) in a constant environment for \( \gamma = 0.6 \) (solid line), \( \gamma = 0.8 \) (dashed line) and \( \gamma = 0.99 \) (dotted line), with \( c_1 = 8 \), \( c_2 = 6 \) and \( c_3 = 5 \). (b) ES allocation towards survival \( \pi^* \) in stochastic environments with increasing variance \( \sigma^2 \), line types are the same as given in (a). (c) ES allocation strategy \( \pi^* \) in stochastic environments defined by different \( \alpha \) values for the same overall variance, \( \sigma^2 = 1 \). When \( \alpha < -0.5 \), there is no stable ES allocation strategy for each value of \( \gamma \). Although strategies on the lower line can invade all others, they can be invaded by strategies in the area between the lower and the upper lines.
Figure 3. (a) ES allocation to survival $\pi^s$ in stochastic environments with increasing variance, for different conversion efficiencies for fecundity, ranging from $c_2=7.5$ (solid line) to $c_2=4$ (dashed line); $\gamma = 0.6$, $c_1 = 8$ and $c_1 = 5$. For high $c_2$, allocation away from survival and towards fecundity is favoured; if $c_2$ is sufficiently low, the ES allocation towards survival increases with increasing variance. (b) The same, but for autocorrelated environments, ranging from $c_2=7.5$ (solid line) to $c_2=6$ (dot-dashed line), with $c_1 = 8$ and $c_1 = 5$. As $c_2$ decreases, ES allocation towards survival increases.

(b) Coexistence and evolutionary stability in environments with strong negative autocorrelation

Since we could not find stable evolutionary outcomes for $\alpha < -0.5$, we used pairwise invasibility plots (pips) to explore evolutionary dynamics and coexistence of competing strategies. We calculated the invasion rate $\psi$ for all possible pairs of resident and invader strategies $\pi_r$ and $\pi_i$, and then created the corresponding pips. Areas where the strategy on the $y$-axis can invade the strategy on the $x$-axis are shown in white in figure 4a. The process of invasion and fixation of mutations. Once all individuals in the population have the phenotype $\pi_o$, no further changes are expected: $\pi_o$ is the ES strategy. However, for values of high negative autocorrelation, there is an area above the main diagonal to the right of the vertical line which is white (figure 4a), indicating more complex outcomes: no value of $\pi$ is un-invadable, so the population is not expected to settle to a monomorphic state.

Pairs of strategies that can stably coexist over ecological time scales (i.e. form protected polymorphisms) occur in areas of overlapping positive invasion rates of residents...
and invaders. Such areas can be identified by taking the mirror image of a pip along its main diagonal and then overlaying it with the original pip to identify areas where both graphs are white. If an invader with resource allocation \( \pi = x \) can invade a resident with resource allocation \( \pi = y \), the point with coordinates \((x, y)\) on the first graph (e.g. figure 4a,c,e) will be white. If \( \pi = y \) is now taken as an invader, and can invade a resident with resource allocation \( \pi = x \), the point with coordinates \((x, y)\) on the mirror image of the first graph (not shown) will also be white. Mutual invasion is a condition for coexistence, so areas where both graphs (the pip and its mirror image) are white will be areas of coexistence. These are shown in figure 4b,d,f. Areas of protected polymorphisms occur for all forms of environmental autocorrelation. The pattern of coexisting pairs does not vary much for \( \alpha > -0.5 \) (figure 4d,f), and all coexisting pairs are invadable by mutants closer to \( \pi_e \). Consequently, for \( \alpha > -0.5 \), although pairs of strategies may coexist on ecological time scales, the population will move towards a monomorphic ES state over evolutionary time, where all individuals have the phenotype \( \pi_e \).

For \( \alpha < -0.5 \), the situation is more complex. The pips indicate that if, initially, all individuals have the same single value of \( \pi_e \), evolution will move the population towards the singular strategy, \( \pi_e \). However, once \( \pi_e \) has been reached, any nearby mutant can invade. What will follow can be established by numerical simulation (evolutionary isoclines (Geritz et al. 1999) are not readily available in our system). We therefore initiated monomorphic populations and every 10 000 time steps, we generated mutants with values of \( \pi \) distributed close to the resident’s \( \pi \), which were introduced into the population at low starting densities. Dynamics of all \( \pi \) strategies coexisting in the population were then tracked for another 10 000 years. If frequency of a given mutant type fell below a chosen threshold (0.4) during this period, we considered that it had gone extinct. The chosen value of the threshold did not affect the results (Geritz et al. 1999). The process was repeated for 1000 introductions. In more than 50 simulations, only two outcomes were observed: (i) evolution towards \( \pi_e \) and then persistence in proximity to it and (ii) evolution towards \( \pi_e \) and then branching and persistence in a dimorphic ES state (figure 5).

4. DISCUSSION

For any organism, resource allocation does not occur in a void: the environmental context modifies outcomes. We explored how this influenced the evolution of allocation strategies for semelparous life histories in constant, temporally varying and autocorrelated environments. Temporal autocorrelation might be especially important for semelparous plants because they frequently inhabit disturbance-driven habitats characterized by successional dynamics which may contribute to autocorrelation (Tuljapurkar & Haridas 2006). Although previous life-history studies have considered temporal autocorrelation (Orzack 1985; Tuljapurkar & Wiener 2000), our focus on allocation strategies and the evolution of survival while including density dependence are novel.

In constant environments, allocation to survival decreases as environmental quality improves (figure 2a), reflecting nonlinearities in survival and environmental quality: beyond a certain level, allocating resources to survival is futile because survival probability saturates at 1 (e.g. Jensen 1906).

In temporally varying environments, existing theory suggests that the ES resource allocation should convey a phenotype that averages over uncertainty in the environment (detailed above). In agreement with this prediction, we found that allocation towards survival is favoured in more variable environments, if allocation towards fecundity leads to small increases in fecundity (small \( c_2 \), additive or multiplicative fecundity). Such survival-oriented allocation strategies maximize fitness by increasing chances of persistence through bad environmental conditions. However, contrary to existing theory, we found that if allocation towards fecundity leads to large increases in fecundity (large \( c_2 \) and multiplicative fecundity), the benefits of fecundity in good environmental conditions are sufficient to overcome the risk of mortality in poor conditions. Consequently, phenotypic strategies that allocate resources away from survival and towards fecundity maximize fitness in more variable environments (figure 2b). Thus, the ES resource allocation depends greatly on how efficiently organisms are able to convert resources into fecundity, likely to be variable across plants and animals.

We also found that increased temporal autocorrelation in the environment always favoured increased allocation towards survival (figure 2c). Temporal autocorrelation describes what the future will hold in a probabilistic way (Orzack 1985; Tuljapurkar & Haridas 2006). In our system, this corresponds to the side of figure 1a,b on which the environment is likely to remain. In bad sequences of years, favouring survival is critical to guarding against extinction. In good sequences of years, favouring survival comes at little loss in terms of fecundity, and can even lead to rewards if conditions continue to improve. Allocation to survival is
thus always optimal. These findings echo recent results of Schwager et al. (2006) who found that environmental variation increases extinction risk by increasing the risk of rare catastrophes, but runs of good years in positively autocorrelated environments diminish the risk of extinction. Temporal autocorrelation may be a crucial component of the environment to consider in evolutionary studies, through its role in both fitness maximization and extinction processes (Lande & Orzack 1988).

Our results relate to real systems in a number of ways. For example, monocarpic plant species such as Arabidopsis thaliana feature trade-offs between growth and survival, both ecological (Mauricio 1998; Mauricio et al. 2003), related to leaf structure (Metcalf et al. 2006) and allocation based (Farnsworth 2004). Such growth processes are captured by the trade-off structure in our model, as reduced growth leads to lower fecundity owing to strong allometric relationships between reproductive output and size (Aarsen & Clauss 1992; Klinkhamer et al. 1992). These fitness losses will be offset by higher survival, and we have shown that the ES allocation depends greatly on environmental conditions. Nevertheless, our model does not consider the benefits of survival due to accumulating benefits of growth across years. This simplification may be appropriate in some cases: for example, Cardusus nutans in Australia showed no relationship between size in 1 year and that in the next year (Rees et al. 2006). The ranking of growth and survival allocation for species inhabiting different environmental conditions characterized by different degrees of variation and autocorrelation could then be predicted. For example, populations living nearest the Atlantic coast of Europe are more likely to be affected by the North Atlantic oscillation than populations in eastern Europe, and thus the former may experience more predictable environments and higher temporal autocorrelation. This prediction could be tested by comparing population demographics across longitudinal gradients (while fixing latitudinal gradient), or better yet, by comparing physiological allocation towards survival-related traits in the laboratory across genotypes collected from a longitudinal gradient in northern Europe.

A growth–survival trade-off has also been suggested to enhance coexistence of phenotypic strategies by flattening fitness landscapes (Mangel & Stamps 2001). Our model indicates that coexistence of a range of strategies is possible in a range of environments, as indicated by the presence of white areas in figure 4b,d,f. However, in most cases, an ES allocation can always invade: polymorphisms are rarely ES, and over evolutionary time scales, populations will eventually become monomorphic. That said, strong negative autocorrelation in the environment over time can lead to the evolution of stable polymorphisms in resource allocation strategies: one with high and one with low allocation to survival (figures 4a and 5). Thus, negatively autocorrelated environments are a potentially important explanation for coexistence of life histories with different mortality schedules.

Although rarely considered, negatively autocorrelated environments may be prevalent in a range of situations. For example, species characterized by several generations within a year experience a negatively autocorrelated environment through seasonal changes. Moreover, a variety of mathematical models of ecological and evolutionary dynamics (Cohen 1995; Laakso et al. 2005) can produce negative temporal autocorrelation. For example, strong density dependence in fast growing populations can trigger negatively autocorrelated fluctuations in population size, and a herbivore with such a life history could create a context in which plants experience such environments, especially if the herbivore affected the mortality rate of the plant species. Delayed density dependence driven by nutrient cycling (e.g. Gonzalez-Andujar et al. 2006) might have similar effects. In such cases, we predict that dynamic coexistence of long-lived and short-lived life-history strategies is possible.

To conclude, although increased allocation to survival may be explained simply as part of a strategy to reap the direct benefits of persistence (e.g. increased size through growth can lead to a larger fecundity reward; Metcalf et al. 2003), here we have shown that even at the cost of reduced fecundity, the variance or autocorrelation structure of environmental conditions alone can select for increased allocation towards survival. Investment in survival can be viewed as a bet on the future, and both degree of variation and autocorrelation in environmental conditions contain information about the future that affects this bet. Given the recent theoretical interest in the role of temporal autocorrelation on population growth rate (Tuljapurkar & Haridas 2006), extinction (Schwager et al. 2006) and now life-history evolution, we encourage empirical study and experimental tests of the role that temporal autocorrelation plays in the evolution of life-history allocation strategies.

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