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_t, where increasing values of X_t 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_t 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 $X_t = 0$, and then generated deviates from a normal distribution with mean 0 and increasing variation to obtain sequences of environmental conditions through time, $\boldsymbol{X}_{\sigma^2}$, such that $\boldsymbol{X}_{\sigma^2} \sim N(0, \sigma_\epsilon)$, for a range of σ_ϵ. 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)

$$X_{t+1} = \alpha X_t + \epsilon_{t+1}, \tag{2.1}$$

where α is the autocorrelation parameter ($|\alpha| < 1$) and ϵ is a normally distributed random variable $\epsilon \sim N(0, \sigma_\epsilon)$ (Schwager *et al*. 2006). We varied α between -0.99 and 0.99 and normalized the resulting sequences, so that $\boldsymbol{X}_\alpha \sim N(0, \sigma_x)$ with $\sigma_x = 1$ (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,

$$\begin{pmatrix} \mathcal{J}_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} P(1-\gamma) & p_e F \\ P\gamma & 0 \end{pmatrix} \begin{pmatrix} \mathcal{J}_t \\ A_t \end{pmatrix}. \tag{2.2}$$

The probability of maturing is denoted by γ; P indicates the probability of survival; F captures fecundity (number of offspring produced); and p_e 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 $\boldsymbol{X}_{\sigma^2}$ or $\boldsymbol{X}_\alpha = [X_1, X_2, X_3, ..., X_T]$. 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 $P = (e^{\pi c_1 + X_t})/(1 + e^{\pi c_1 + X_t})$ to constrain survival between 0 and 1, and $F = e^{(1-\pi)c_2 + X_t}$, where X_t is the value of the environment at time t and π 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 π as a phenotypic strategy; the chosen strategy or value of π controls the allocation of resources between survival and fecundity (i.e. the trade-off strategy). We assume that π is under genetic control, and then evaluate the values of π 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).
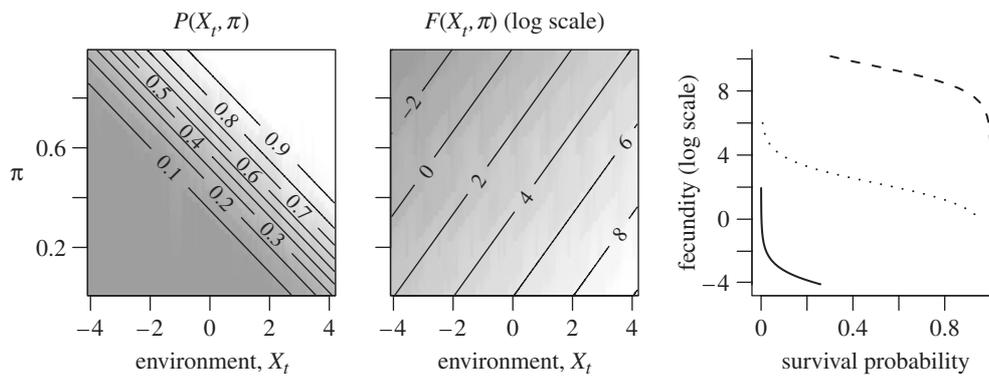
Figure 1. (a) Landscape of survival probability, $P = (e^{\pi c_1 + X_t - c_3})/(1 + e^{\pi c_1 + X_t - c_3})$ (see text) across the range of possible allocation strategies π and environmental conditions X_t, taken with $c_1 = 8$ and $c_3 = 5$. Decreasing c_1 decreases the slope of the landscape in the plane of π. Decreasing c_3 shifts the landscape to the right. (b) Landscape of fecundity $F = e^{(1-\pi)c_2 + X_t}$ with $c_2 = 6$. Decreasing c_2 decreases the slope in the plane of π. 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 π, for the worst environment, X_t (represented by a solid line), mean environment (dotted line) and best environment (dashed line).

Such 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 slopes 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 π 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 $P = (e^{\pi c_1 + X_t - c_3})/(1 + e^{\pi c_1 + X_t - c_3})$ 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_α or X_{σ^2}. 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 π, 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 π for a range of values of X_t between -4 and 4. The value of π corresponding to the maximal R_0 identifies the constant environment ES π for that X, denoted by π_X^*.

(ii) Stochastic environments

In a stochastic environment, evolutionary dynamics is regulated by the stochastic growth rate ϑ of an invader into an environment determined by the resident strategy π_r in a context defined by environmental conditions over time X_{σ^2} or X_α (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 π_r. 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:

$$p_{e,r}(t) = \frac{M_{t+1}}{A_{r,t} e^{(1-\pi_r)c_2 + X_t}},$$
(2.3)

where the subscript r 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 $A_{r,t}$ is the number of resident adults in time step t. The denominator in (2.3) is therefore the total number
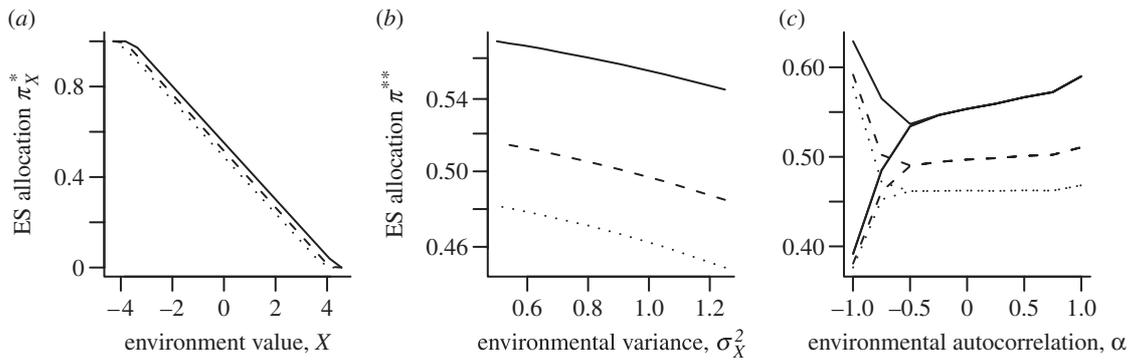
Figure 2. (a) ES allocation towards survival π_X^* in a constant environment for $\gamma = 0.6$ (solid line), $\gamma = 0.8$ (dashed line) and $\gamma = 0.99$ (dotted line), with $c_1 = 8$, $c_2 = 6$ and $c_3 = 5$. (b) ES allocation towards survival π^{**} in stochastic environments with increasing variance σ_X^2, line types are the same as given in (a). (c) ES allocation strategy π^{**} in stochastic environments defined by different α values for the same overall variance, $\sigma_X^2 = 1$. When $\alpha < -0.5$, there is no stable ES allocation strategy for each value of γ. 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.

of offspring produced by all resident adults at t, where the resident's allocation strategy is π_r. Since the probability of establishment for the invader's offspring in each time step is determined entirely by the number of offspring produced by the resident, it is also given by (2.3): $p_{e,i}(t) = p_{e,r}(t)$. By incorporating (2.3) into (2.2), we obtain the matrix and equation defining the invader's dynamics,

$$\begin{pmatrix} \mathcal{J}_{i,t+1} \\ A_{i,t+1} \end{pmatrix} = \begin{pmatrix} P_{i,t}(1-\gamma) & p_{e,i}(t)F_{i,t} \\ P_{i,t}\gamma & 0 \end{pmatrix} \begin{pmatrix} \mathcal{J}_{i,t} \\ A_{i,t} \end{pmatrix}. \quad (2.4)$$

By iterating (2.4) over time, the invader's rate of invasion ϑ can be estimated from

$$\vartheta = \lim_{t \to \infty} t^{-1} E[\ln(N_{i,t})], \quad (2.5)$$

where $N_{i,t} = \mathcal{J}_{i,t} + A_{i,t}$ is the invader's total population size at time t (Metz 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_α or X_{σ^2}, where T is sufficiently large to approximate dynamics at ∞. We calculated and stored the resulting $p_{e,r}(t)$ at every time step following (2.3). We then invaded this resident by a range of invading strategies ($0 \leq \pi_i \leq 1$), whose dynamics were defined by X_α or X_{σ^2}, $p_{e,i}(t)$, which is equal to $p_{e,r}(t)$ in (2.3), and (2.4). If $\vartheta \leq 0$ 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. We iterated the procedure described previously until we identified the strategy that could not be invaded by any other strategy, which is the ES allocation strategy, π^{**}. In some cases, no π^{**} could be identified. For these cases, to explore dynamics and assess whether different strategies could coexist or not, we used an adaptive dynamics approach. This involved plotting out invasion success or failure for all possible combinations of resident and invasion allocation strategies (Geritz et al. 1997).

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 π 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_2 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. γ 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 sensitive 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.

(iii) *Stochastic environments with different degrees of autocorrelation*
Where the degree of temporal variation in the environment did not change, and the environment became more positively autocorrelated, the ES allocation
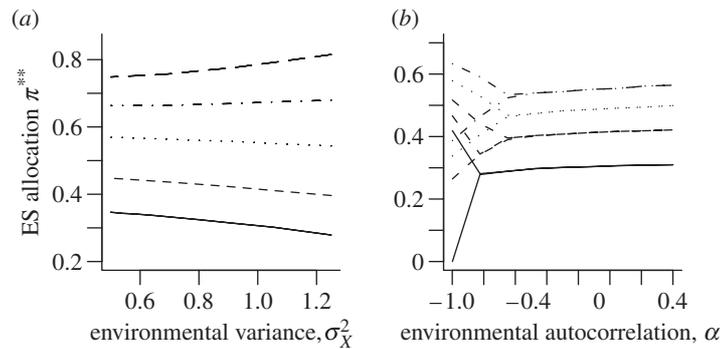
Figure 3. (*a*) ES allocation to survival π^{**} in stochastic environments with increasing variance, for different conversion efficiencies for fecundity, ranging from $c_2 = 7.5$ (solid line) to $c_2 = 4$ (dashed line); $\gamma = 0.6$, $c_1 = 8$ and $c_3 = 5$. For high c_2, allocation away from survival 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 $c_3 = 5$. As c_2 decreases, ES allocation towards survival increases.

towards survival increased (figure 2*c*). The slope of this increase was greater for low maturation probabilities, γ. Interestingly, when the environment was negatively autocorrelated, with $\alpha < -0.5$, there was a strategy that could invade all other strategies (figure 2*c*, lower lines), but it could be invaded by strategies with higher allocation to survival. There was therefore no single ES allocation strategy. For higher maturation probabilities, γ, the same overall relationship was retained, but, as above, the investment in survival was lower.

Across a range of c_1 and c_2 values, the qualitative relationship between ES allocation to survival and the degree of environmental autocorrelation (figure 2*c*) was retained. For c_1, the quantitative change was in the same direction as for increasing environmental variability: higher c_1 values led to higher ES allocation towards survival (not shown). Higher c_2 led to decreased allocation towards survival (figure 3*b*). If additive rather than multiplicative fecundity model was used, results remained qualitatively the same.

(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 ϑ for all possible pairs of resident and invader strategies π_r and π_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 4*a,c,e*; where it cannot and goes extinct are shaded. On the diagonal crossing the graph from bottom left to top right, the resident's strategy is equal to the invader's, and therefore $\vartheta = 0$, as the resident is at equilibrium. The intersection of this diagonal with the line separating areas with positive and negative invasion rates represents the 'singular strategy' π_s, around which evolutionary dynamics revolve (Geritz *et al.* 1999).

For all X_α, a horizontal line through π_s is entirely within the white area, meaning that π_s can invade any other value of π (figure 4*a,c,e*). For most X_α, the area above the main diagonal to the left of the vertical line and below the main diagonal to the right of the vertical line is white, indicating that any resident strategy can be invaded by a mutant closer to π_s (figure 4*b,c*). Over evolutionary time, these populations are therefore expected to move towards π_s by an iterative
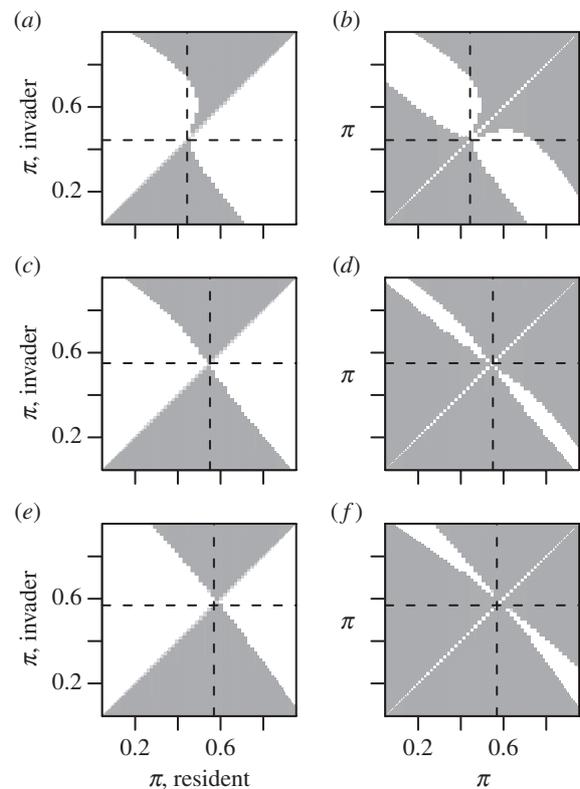
Figure 4. (*a,c,e*) Pips for different X_α, with $c_1 = 8$, $c_2 = 6$ and $c_3 = 5$, and $\alpha = -0.99$, 0 and 0.99, respectively; areas in white correspond to successful invasion by the strategy on the *y*-axis into an environment set by the strategy on the *x*-axis. (*b,d,f*) Corresponding areas of coexistence (in white). Dashed vertical and horizontal lines indicate the singular strategy. For (*a*), the singular strategy, π_s, is invasible and therefore unstable, indicated by the dashed vertical line being in white area.

process of invasion and fixation of mutations. Once all individuals in the population have the phenotype π_s, no further changes are expected: π_s 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 4*a*), indicating more complex outcomes: no value of π 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 π_s. 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 π_s.

For $\alpha < -0.5$, the situation is more complex. The pips indicate that if, initially, all individuals have the same single value of π, evolution will move the population towards the singular strategy, π_s. However, once π_s 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 π distributed close to the resident's π, which were introduced into the population at low starting densities. Dynamics of all π 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 π_s and then persistence in proximity to it and (ii) evolution towards π_s 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
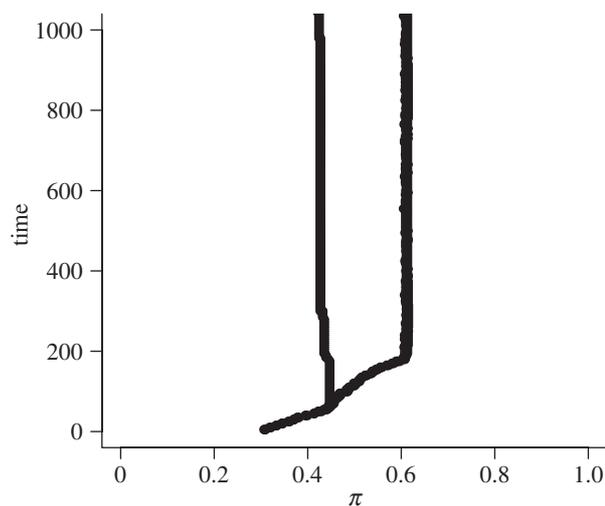
Figure 5. Simulated evolutionary tree for a population in a negatively autocorrelated environment ($\alpha = -0.99$), $c_1 = 8$, $c_2 = 6$, $c_3 = 5$, and starting with all individuals having a $\pi = 0.3$. Every 10 000 years, mutants with values of π taken from a distribution around the resident strategies are introduced at very low densities. The population reaches the singular strategy, π_s, and undergoes disruptive selection, finally settling in a dimorphic ES state. Simulations all either ended up in this state or continued in a monomorphic state with $\pi \sim 0.41$, corresponding to π_s for this environment.

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 (Aarssen & 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, *Carduus 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 4*b*,*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 4*a* 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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