JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.12474

Why wait? Three mechanisms selecting for environment-dependent developmental delays

M. F. SCOTT* & S. P. OTTO†

*Department of Botany, University of British Columbia, Vancouver, BC, Canada
†Department of Zoology, University of British Columbia, Vancouver, BC, Canada

Keywords:

developmental delays;
disturbance;
environmental variation;
germination strategies;
life-history evolution;
modelling;
seed dormancy;
serotiny.

Abstract

Many species delay development unless particular environments or rare disturbance events occur. How can such a strategy be favoured over continued development? Typically, it is assumed that continued development (e.g. germination) is not advantageous in environments that have low juvenile/seedling survival (mechanism 1), either due to abiotic or competitive effects. However, it has not previously been shown how low early survival must be in order to favour environment-specific developmental delays for long-lived species. Using seed dormancy as an example of developmental delays, we identify a threshold level of seedling survival in 'bad' environments below which selection can favour germination that is limited to 'good' environments. This can be used to evaluate whether observed differences in seedling survival are sufficient to favour conditional germination. We also present mathematical models that demonstrate two other, often overlooked, mechanisms that can favour conditional germination in the absence of differences in seedling survival. Specifically, physiological trade-offs can make it difficult to have germination rates that are equally high in all environments (mechanism 2). We show that such trade-offs can either favour conditional germination or intermediate (mixed) strategies, depending on the trade-off shape. Finally, germination in every year increases the likelihood that some individuals are killed in population-scale disturbances before reproducing; it can thus be favourable to only germinate immediately after a disturbance (mechanism 3). We demonstrate how demographic data can be used to evaluate these selection pressures. By presenting these three mechanisms and the conditions that favour conditional germination in each case, we provide three hypotheses that can be tested as explanations for the evolution of environment-dependent developmental delays.

Introduction

One might expect organisms to reproduce as early as possible, yet many organisms delay development such that their eventual reproduction is also delayed, a strategy that should typically lead to a slower growth rate (Rees, 1996). This is the classic evolutionary problem posed by developmental delays (Tuljapurkar & Wiener, 2000), such as seed, spore and cyst dormancy in plants, fungi and bacteria (Cohen, 1967; Ellner, 1985a; Rees, 1996), nonseed ('prolonged' or 'vegetative') dormancy in plants (Roerdink, 1988; Gremer *et al.*, 2012) and diapause in insects, crustaceans, sponges and fish (Tuljapurkar & Istock, 1993; Evans & Dennehy, 2005; Venable, 2007). In this study, we consider the evolution of strategies that delay development in a manner that depends on environmental state in a demographically structured population. First, we briefly review previous studies that explore the evolution of developmental delays and then place our work in this context.

Two classic studies of seed dormancy in annual plants are the influential theoretical papers by Cohen (1966, 1967). Cohen (1966) constrained germination rate to

Correspondence: Michael F. Scott, Department of Botany, The University of British Columbia, 6270 University Boulevard, Vancouver, BC, Canada V6T 1Z4. Tel.: 604 822 2778; fax: 604 822 6089; e-mail: mfscott@biodiversity.ubc.ca

be the same in all years (constant germination strategy) but allowed the seed yield produced per germinating seed to vary across years. The optimal germination strategy was found to depend on the variation in yield across years. If, in some years, yield is lower than survival in the soil, partial seed dormancy can evolve. Cohen (1967) considered a different scenario, in which germination strategy can vary according to the environment at the time of germination (state-dependent germination strategy, sometimes called 'predictive germination', Venable & Lawlor, 1980). If seeds are able to perfectly predict eventual yield based on the environment they experience, germination should occur in 'good' years and dormancy in 'bad' years. If the yield cannot be accurately predicted at the time of germination, then the optimal germination rate in a particular perceived environment depends on the distribution of yields that might actually occur; this set can include some 'good' and some 'bad' yields, in which case intermediate germination rates can again evolve. See the Model Background section for some mathematical details of these models.

Related studies have modelled the timing of diapause in insects and crustaceans in which the diapausing fraction can vary over a year in response to temperature and day length cues (Cohen, 1970; Taylor, 1980; Hairston & Munns, 1984; Taylor & Spalding, 1989; Spencer & Colegrave, 2001). This is equivalent to an extremely plastic germination strategy, and these studies similarly find that populations should switch from nondiapausing to diapausing when the reproductive yield from breaking diapause is lower than the survival of a diapausing individual. For example, Taylor (1980) found that diapause should begin when the time until catastrophe (frost) is less than the time required to reach maturation and produce one offspring of diapausing age. This result assumes that the date of the first frost is predictable. In reality, catastrophes do not reliably occur on the same date each year. Consequently, there is variation in reproductive yield on each day, which can favour a mixed diapause strategy (Cohen, 1970; Hairston & Munns, 1984; Taylor & Spalding, 1989; Spencer & Colegrave, 2001).

The above models correspond to annual plant and diapausing insect life cycles in which only individuals of a single age class persist between years. This allows the demographic dynamics to be described by a single equation: the number of seeds, diapausing eggs, larvae, pupae or adults that overwinter. However, developmental delays are also common in species with overlapping generations. For example, although not explicitly comparing germination rates in annuals and perennials, Baskin & Baskin (2014) find that the percentage of tree or shrub species with some form of seed dormancy is generally similar to the percentage of herbaceous species with dormancy (Figures 12.3 and 12.4) in a review of over 13 000 species. With overlapping generations, demographic modelling becomes more complex because survival and reproduction of each age (or stage) class must be considered. Conceptually, a key difference is that lifetime reproductive output must be calculated over several time steps and so may include several environments and the particular order of those environments.

Nevertheless, there have been some studies that have considered the evolution of developmental delays in age- or stage-structured populations experiencing temporally varying environments. These studies generally consider environmental variation that affects fertility (seed yield) only (but see Koons *et al.*, 2008, discussed below) and assume that strategies do not depend on the environment. Roerdink (1988, 1989) modelled the evolution of delayed reproduction in a predominantly biennial species that dies after reproducing. Similarly, Tuljapurkar (1990) presented a model for the evolution of delayed reproduction in semelparous organisms and organisms with a very short adult lifespan. Additionally, Tuljapurkar & Istock (1993) considered the evolution of a short developmental delay, for example diapause in insects that can delay maturation for 1 year only. These studies have shown that delays can evolve in a demographically structured population to buffer against environmental variability in fertility, as in the unstructured model considered by Cohen (1966).

Developmental delays spread the reproductive effort from a seed/juvenile cohort over time, providing an 'escape in time' from environmental variation (Venable & Lawlor, 1980). Iteroparity also spreads reproductive effort over time, buffering against environmental variation even in the absence of developmental delays (Tuljapurkar & Istock, 1993; Tuljapurkar & Wiener, 2000). Developmental delays can evolve in an iteroparous population, providing both forms of buffering, but only if mean seed (juvenile) survival is higher than mean adult survival and thus seeds (juveniles) are able to 'spread the risk' more than iteroparity alone (Koons *et al.*, 2008). Tuljapurkar & Wiener (2000) also explored the evolution of both iteroparity and developmental delays, assuming a linear trade-off between adult survival and yearly reproductive effort. They tended to find either the evolution of iteroparity or developmental delays, but other trade-off functions might generate simultaneous selection for a mixture of iteroparity and developmental delays (as suggested by Wilbur & Rudolf, 2006).

The above studies for demographically structured populations all assume a constant strategy in all years, as in Cohen (1966). Here, we model the evolution of a state-dependent strategy in a demographically structured population, that is germination rate can be different in different environments. The case where cues allow the strategy to depend on the time of year has been considered in models for the timing of diapause

(Taylor, 1980; Hairston & Munns, 1984; Spencer & Colegrave, 2001). However, particular environments can provide cues that allow germination rates to vary in a state-dependent (not time-dependent) manner. Examples of state-dependent developmental delays include seed germination responses to light and rainfall (Pake & Venable, 1996; Evans *et al.*, 2007) or spore germination responses to heatshock (Perkins & Turner, 1988), amino acid concentrations or host-specific substances (Cohen, 1967). In a particularly clear example, smoke or temperature cues from fires cause increased germination rates or release of seeds from fruiting structures ('serotiny') in many species (including many perennials, Keeley, 1995). Treatment with smoke is estimated to increase germination rates in over 2500 species (Bradshaw *et al.*, 2011), and up to 1200 perennials exhibit serotiny (Lamont *et al.*, 1991; Lamont & Enright, 2000).

For simplicity, we will use botanical terms (seeds, germination, etc.), although the models themselves can apply to other developmental delays that depend on environmental state. As discussed above and elsewhere (Rees, 1996; Evans *et al.*, 2007), the evolutionary problem posed by dormancy is that delaying development eventually delays reproduction and so reproductive opportunities seem to be passed up. In this context, the problem of conditional germination strategies is not 'Why germinate in environment 1?' but 'Why forgo germination in environment 2?'.

In this work, we investigate this problem and present three mechanisms generating selection that favours organisms that pass up germination opportunities: (1) Avoiding germination in 'bad' environments that have low seedling survival. (2) Avoiding costly physiological trade-offs between the germination rates in different environments (in addition to the fundamental 'trade-off' that seeds that germinate are no longer available to germinate in the future). (3) Minimizing the risk of experiencing a severe disturbance before reproducing (note that this requires state-dependent germination and perenniality).

This provides a framework for researchers wishing to investigate the evolution of environment-dependent developmental delays. We provide a threshold level of seedling survival in 'bad' environments below which conditional germination should evolve, thus providing a quantitative means to test whether the most commonly envisaged mechanism can explain the evolution of conditional germination in a particular organism. If not (or if there are also physiological trade-offs or large-scale disturbances), we point out that the other, less commonly discussed, mechanisms should be considered. With demographic data for a particular species in different environments, one can investigate whether these selective mechanisms should act by manipulating the relevant parameters separately as we do here. For example, setting seedling survival in all environments to be equivalent eliminates mechanism 1 and reducing the number of years required to reach maturity can eliminate mechanism 3. We discuss some specific empirical data for these mechanisms in more detail in the Discussion section.

Model background

To connect our model with previous results, we first provide a brief overview of some key mathematical results. In the model by Cohen (1966), the number of seeds (S) at time t is given by

$$S[t] = S[0]\left(\prod_i ((1-g)s_S + gy_i)^{p_i}\right)^t, \qquad (1)$$

where g is the germination rate (assumed constant), s_S is the survival of seeds in the soil, and p_i is the proportion of the t years that has environment i in which the environment-specific seed yield is y_i. Increasing germination rate will increase (decrease) growth rate if the derivative of the parenthetical term with respect to g is positive (negative), where the sign of this derivative depends on $\sum_i (p_i(y_i - s_S))/((1-g)s_S + gy_i)$. Dormancy may evolve if some years yield fewer seeds than would survive in the soil ($y_i < s_S$). For example, a population that germinates 100% of its seeds would go extinct if ever an extremely 'bad' year (no seed set) were encountered, favouring the evolution of seed dormancy.

Where environments vary over space, however, lineages can escape extinction by surviving in 'good' environments and recolonizing. This has been called 'escape in space' via dispersal in contrast to 'escape in time' via dormancy (Venable & Lawlor, 1980). MacArthur (1972, p. 165–168) introduced a model with many patches and global dispersal among them, finding that the optimal strategy is the one that has the highest growth rate averaged over all patches. In this model, a proportion of the population experiences each environment in each year and so

$$S[t] = S[0]\left(\sum_i p_i((1-g)s_S + gy_i)\right)^t, \qquad (2)$$

where p_i is the proportion of the population that experiences environment i with yield y_i. In this model, changes in germination rate affect growth rate according to the sign of $\sum_i p_i(y_i - s_S)$, which must be positive in a population capable of growth; therefore, seed dormancy should not evolve. These two models, with variability entirely temporal or spatial, are extreme cases, and intermediate scenarios have been considered by others (Levin *et al.*, 1984; Cohen & Levin, 1987; Klinkhamer *et al.*, 1987; Wiener & Tuljapurkar, 1994), who also find that 'escape in space' via dispersal lessens the need for 'escape in time' via dormancy.

Closer to the models we consider, Cohen (1967) includes environment-specific germination into equation (1):

$$S[t] = S[0]\left(\prod_i((1-g_i)s_S + g_iy_j)^{p_{ij}}\right)^t, \tag{3}$$

where g_i is the germination rate in a particular seed environment, and p_{ij} is the proportion of years that seeds are in environment i and yield y_j seeds if germinated. Selection on the germination rate in a particular environment (g_i) then has the same sign as $\sum_{ij}(p_{ij}(y_j - s_S))/((1-g_i)s_S + g_iy_j)$. Germination rate in each environment therefore evolves in a similar manner to the overall germination rate in the Cohen (1966) model. However, each seed environment can have a different optimum. In a special case (termed 'complete information'), the yield is reliably given by the seed environment (i), such that p_{ij} and y_j can be replaced by p_i and y_i. In this case, the pure strategies of complete germination ($g_i = 1$) and complete dormancy ($g_i = 0$) are favoured in 'good' ($y_i > s_S$) and 'bad' ($y_i < s_S$) environments, respectively.

MacArthur (1972) did not include environment-specific germination rates into his model with purely spatial environmental variation. However, one can modify equation (2) to allow germination rate to vary along with the environment that affects seed yield, such that g becomes g_i. This modification may seem equivalent to the 'complete information' case in Cohen (1967), but it also applies with uncertain assessment of yield if y_i is defined as the average yield from seeds across environments – correctly or incorrectly – assessed as being in state i. Although the yield in each patch is uncertain, this uncertainty can be averaged across the patches in each year to give a particular yield for each seed environment. This model also predicts complete germination in 'good' ($y_i < s_S$) patches and dormancy in 'bad' ($y_i < s_S$) patches.

In this study, we consider perennial species and assume that a fixed proportion of the population experiences each environment in each time step in sections 1 and 2 (mechanisms 1 and 2), as in the annual plant model by MacArthur (1972 p165–168). We use the approach explained above to include environment-specific germination rates. In the final section, we include temporal variation where the whole population experiences the same environment in each time step, as in Cohen (1966, 1967). To deal with temporal variation in a demographically structured population, we first consider strictly periodic disturbances to obtain some approximate analytical results and then use numerical simulations based on the demography of *Banksia hookeriana* (following Enright *et al.*, 1998) to investigate the evolution of environment-dependent developmental delays with nonperiodic disturbances. For this section, we consider the 'complete information' case because we focus on the effects of disturbance risk rather than uncertain assessment of yield. That said, when disturbances are nonperiodic, we incorporate uncertainty in the ordering of environments even though the demographic parameters in each environment are constant.

Model and results

We evaluate the evolution of environment-dependent germination (conditional germination) with a variety of stage-structured models. A *Mathematica* (Wolfram Research Inc., 2010) file for replicating our analyses is available as supplementary material. We considered environmental variation that can affect all life-history parameters. In our notation for environment i, the survival of adult plants is s_{Ai}, seed survival is s_{Si}, germination rate is g_i, post-germination seedling survival is s_{Yi} and each adult produces b_i seeds in each time step. We allow both seeds (S) and adults (A) to survive between time steps.

Mechanism 1: Low seedling survival in some environments

It is commonly thought that conditional germination evolves to avoid germination in environments with low seedling survival (e.g. Lamont *et al.*, 1991; Lamont & Enright, 2000; Midgley, 2000; Keeley *et al.*, 2011). To test this mechanism, we first modelled a population in which a random proportion of the population (p_i) experience each environment in each time step ($\sum_{i=1}^{n} p_i = 1$, where n is the total number of environments), with no temporal autocorrelations in patch type (either because migration is global or patches change randomly at each time step). Initially, we examine a density-independent growth model, but we then show that similar conditions arise with a density-dependent model. The changes in seed and adult population sizes from time step t to time t+1 are described by the following recursion equations written in matrix form:

$$\begin{pmatrix} S[t+1] \\ A[t+1] \end{pmatrix} = \mathbf{T_A}\begin{pmatrix} S[t] \\ A[t] \end{pmatrix}, \tag{4}$$

where

$$\mathbf{T_A} = \begin{pmatrix} \sum_{i=1}^{n} p_i s_{Si}(1-g_i) & \sum_{i=1}^{n} p_i b_i \\ \sum_{i=1}^{n} p_i s_{Yi} g_i & \sum_{i=1}^{n} p_i s_{Ai} \end{pmatrix}. \tag{5}$$

We used the leading eigenvalue (λ) of the transition matrix, $\mathbf{T_A}$, to approximate the long-term growth rate of the population of seeds and adults. Then, we examined whether mutants that alter the germination parameters (g_i) have an increased or decreased long-term growth rate. A small change in the germination rate in environment j, g_j, will affect the long-term growth rate, λ, according to

$$\frac{\partial \lambda}{\partial g_j} = \frac{p_j s_{Sj} \sum_{i=1}^{n} p_i s_{Ai} + p_j s_{Yj} \sum_{i=1}^{n} p_i b_i - p_j s_{Sj} \lambda}{2\lambda - \sum_{i=1}^{n} p_i s_{Ai} - \sum_{i=1}^{n} p_i s_{Si}(1 - g_i)}. \qquad (6)$$

Unlike an annual plant version of the same model, equation (6) has terms from all n environments. That is, optimal germination rate in environment j depends on the quality of the other environments that adults might subsequently experience when demographic structure is included. If equation (6) is positive for some environments (j) and negative for others, then conditional germination is expected to evolve. From this point on, we will focus on the case where environments can be classified into two groups. Two is the minimum number of environments required for conditional germination, in which dormancy is favoured in one environment but not another.

In this section, we demonstrate that differences in seedling survival can favour conditional germination. For this purpose, we define a 'good' ($i = 1$) patch as one in which seedling survival is higher than in the 'bad' ($i = 2$) patches ($s_{Y1} > s_{Y2}$). Assuming that the population is capable of growth ($\lambda > 1$), germination rates in the 'good' environment should always be maximized (mutants with higher g_1 values always have high higher long-term growth rates). By contrast, germination rates in the 'bad' environments (g_2) should sometimes evolve to be as high as possible and sometimes as low as possible, with the transition occurring when the following condition holds:

$$\frac{s_{Y2}(b_2 s_{Y2} + s_{A2} - s_{S2})}{g_1 s_{S1}(s_{Y1} - s_{Y2}) + s_{Y2}(s_{Y2}(b_2 - b_1) + s_{A2} - s_{A1} + s_{S1} - s_{S2})} - p = 0, \qquad (7)$$

where we have specified that the 'good' ($i = 1$) environment is experience by p proportion of the population and the 'bad' ($i = 2$) environment by ($1-p$). See Appendix S1 for more details of our analysis. An example of how the long-term growth rate (λ) changes on either side of this point is shown in Fig. 1a.

Figure 1b illustrates the region in which conditional germination is expected to evolve, with germination only occurring in 'good' patches. The proportion of 'good' patches (p) must be high enough, and seedling survival in 'bad' patches (s_{Y2}) must be sufficiently low. When seedling survival in both environments is equivalent (dashed line in Fig. 1b), conditional germination should never evolve in populations capable of growth ($\lambda > 1$). It has previously been noted that conditional germination should evolve when establishment ability in 'bad' environments is negligible ($s_{Y2} = 0$, Lamont *et al.*, 1991). Equation (7) echoes this result but also

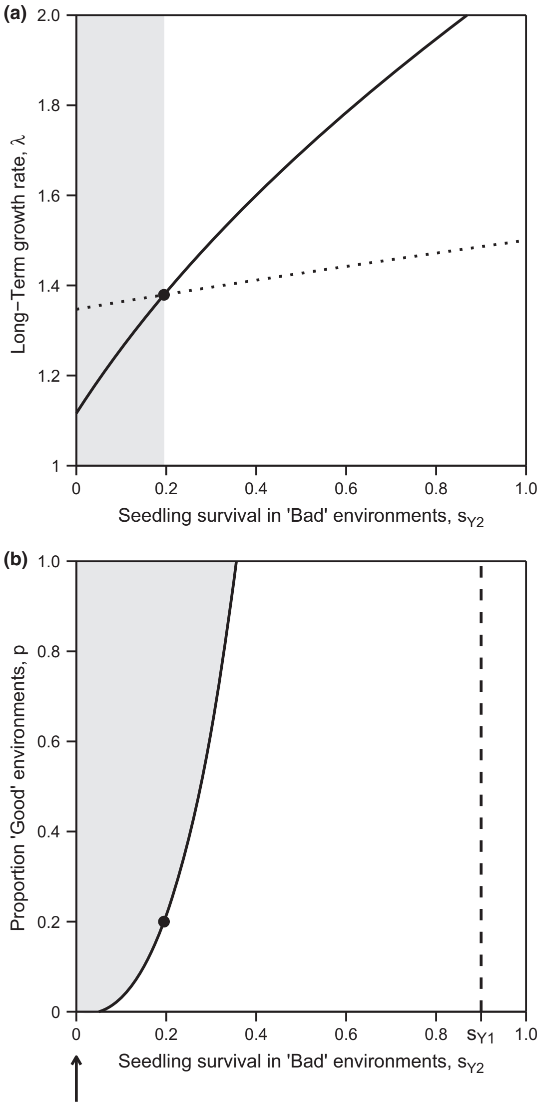

Fig. 1 Life-history parameters for which conditional germination strategies have a higher long-term growth rate. (a) The long-term growth rate (λ) for a plant with a conditional germination strategy (dotted line, $g_2 = 0.1$) and a plant without one (black line, $g_2 = 1$). Conditional germination confers a higher growth rate when seedling survival is below the transition point specified by equation (7) (circle). The grey region shows where conditional germination is expected to evolve. (b) When the frequency of 'good' environments (p) is high enough and the seedling survivorship in bad years (s_{Y2}) is low enough, conditional germination should evolve (grey). If seedlings never establish in 'bad' years ($s_{Y2} = 0$, see arrow), a plant always falls in the region favouring conditional germination (grey). The dashed line indicates where seedling survival is equal across 'good' and 'bad' years ($s_{Y1} = s_{Y2}$), in which case conditional germination never evolves (see Appendix S1). Note that, even where selection would favour germination if only the 'bad' environment were experienced (see white region along x-axis, $p = 0$), conditional germination can evolve. The other parameters used are $g_1 = 1$, $p = 0.2$, $s_{Y1} = 0.9$, $s_{S1} = 0.8$, $s_{S2} = 0.8$, $b_1 = b_2 = 4$, $s_{A1} = 0.6$, $s_{A2} = 0.6$.

shows a more general case, in which we indicate exactly how low seedling survival in 'bad' patches (s_{Y2}) must be.

In Appendix S1, we also show that the region in which conditional germination should evolve expands when the seed bank is more persistent (s_{Si} is larger), the proportion of the population experiencing 'good' conditions (p) is larger and when germination rate (g_1) and seedling survival (s_{Y1}) in good patches is higher. In contrast, this region will contract when adult survival (s_{Ai}) is higher, number of seeds produced (b_i) is higher, or when seedling survival in 'bad' years (s_{Y2}) is higher.

Mechanism 2: Trade-offs

In the above model and MacArthur (1972), germination rates evolve to be either maximized or minimized. We next include physiological trade-offs, which can allow intermediate germination rates to evolve even with purely spatial variation in environments. This is true for both annual and perennial plant models (see Appendix S2 for a version of the MacArthur (1972) annual plant model with trade-offs, which produces very similar results to the perennial model presented here). Trade-offs could exist between any of the demographic parameters, see the Discussion section for some examples, but to demonstrate the qualitative effects of trade-offs on germination rate, we incorporated a direct trade-off between germination rates in different environments (g_1 and g_2) using a generic function ($g_1[g_2]$). For two types of patches and global migration, the transition matrix describing changes in seed and adult populations then becomes:

$$\mathbf{T_B} = \begin{pmatrix} p s_{S1}(1-g_1[g_2]) + (1-p) s_{S2}(1-g_2) & p b_1 + (1-p) b_2 \\ p s_{S1} s_{Y1} g_1[g_2] + (1-p) s_{S2} s_{Y2} g_2 & p s_{A1} + (1-p) s_{A2} \end{pmatrix}. \tag{8}$$

Here, we are particularly interested in cases where conditional germination is expected to evolve where it would not without the trade-off. Therefore, we start by presenting the special case of (8) where seedling survival is constant ($s_{Y1} = s_{Y2}$), which never yielded conditional germination strategies in the previous section.

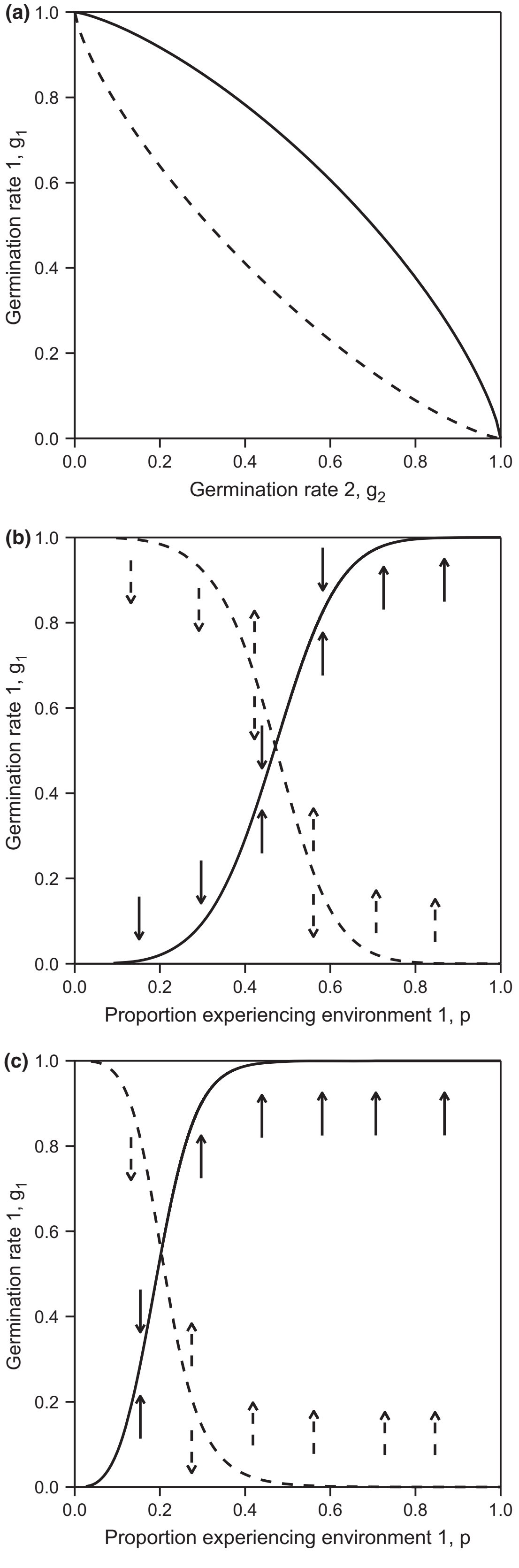

Fig. 2 Trade-offs between germination rates (g_1 and g_2) can favour intermediate strategies or specialization. Panel (a) shows a concave (solid, $s = 4/3$) and convex (dashed, $s = 3/4$) example for the trade-off function using $g_1[g_2] = 1 - (1 - (1 - g_2)^{1/s})^s$. Panels (b) and (c) show the corresponding evolutionarily stable germination strategy (solid) or the repelling strategy (dashed), with arrows representing the expected evolutionary trajectory for germination rate for a given frequency of environments 1 (p) vs. 2 ($1-p$). Panel (b) assumes $s_{Y2} = s_{Y1}$ (corresponding to the dashed line in Fig. 1b), in which case the curves are given by equation (9). Panel (c) shows an example where $s_{Y2} \neq s_{Y1}$ ($s_{Y1} = 0.9$, $s_{Y2} = 0.4$). Other parameters in (b) and (c) are as in Fig. 1.

Our approach (details in Appendix S2) was to identify evolutionarily stable strategies (ESS) for germination rates (g_1 and g_2) where no mutant would have a higher growth rate, λ. For model (8) with $s_{Y1} = s_{Y2}$, a singular point occurs when

$$\frac{s_{S2}}{s_{S2} - s_{S1} g_1{}'[g_2]} - p = 0 \qquad (9)$$

where $g_1{}'[g_2]$ is the first derivative of the trade-off function. In some cases, traits that maximize germination rate in one environment could also increase germination rates in other environments (e.g. Simons, 2014). If germination rates are positively coupled in this manner ($g_1{}'[g_2] > 0$), the singular point in (9) cannot be satisfied and germination rates should evolve to be high. However, in Fig. 2b, we plot equation (9) for a negative trade-off (where physiological constraints make it difficult to have simultaneously high germination rates in all environments, $g_1{}'[g_2] < 0$). We next determined whether this singular point is a maximum or a minimum growth rate to assess whether germination rates are expected to evolve towards this point or away (whether it is an ESS or evolutionary repeller). We found that singular point (9) changes from an ESS to an evolutionary repeller when the shape of the trade-off function transitions between concave ($g_1{}''[g_2] < 0$) and convex ($g_1{}''[g_2] > 0$), see Fig. 2.

When trade-offs are concave (solid line in Fig. 2), seeds are able to germinate reasonably well in both environments, and the germination strategy is expected to reach an intermediate ESS germination rate in both environments, where the two germination rates satisfy equation (9). Observing intermediate germination rates could then suggest the presence of a trade-off (e.g. Tonnabel *et al.*, 2012, discussed below) or temporal variation (see next section).

With a convex (dashed line in Fig. 2) trade-off, plants are expected to specialize on germination in either environment 1 or 2. Thus, conditional germination can evolve as a means to specialize and avoid a costly trade-off. The germination strategy predicted to evolve with a convex trade-off depends on seed survival rates (s_{Si}), the proportion of patch types 1 vs. 2 and any initial specialization. Importantly, though, even if survival and fertility are equal in all environments, conditional germination can still evolve, simply because the traits that allow good germination in one environment prevent it in the other. Empirically then, trade-offs are likely present in cases where little difference in demographic parameters can be detected.

We next combine the effects of a trade-off with differences in seedling survival (mechanisms 1 and 2). As in the previous section, we arbitrarily assume that environment 1 has superior seedling survival ($s_{Y1} > s_{Y2}$). When $s_{Y2} \neq s_{Y1}$, the simple solution (9) no longer applies. We obtained a more complicated expression for the singular point (ESS or repeller) and plotted an example in Fig. 2c. What is apparent is that, decreasing seedling survival in 'bad' environments (s_{Y2}) increases the region of parameter space over which germination rates in the 'bad' environments should evolve to be low.

The above models ignore competition and assess growth rates of different life-history strategies. We next incorporated density dependence into this model by including a competition function that limits population size. For example, competition-related mortality might affect seedling survival such that the lower left element in matrix $\mathbf{T_B}$ is multiplied by the logistic density-dependent function ($1 - \frac{A[t]}{K}$) where K is the population carrying capacity of adults. More generally, we multiplied seedling survival by an arbitrary competition function ($comp[A[t]]$) to re-write the transition matrix as:

$$\mathbf{T_C} = \begin{pmatrix} p s_{S1}(1 - g_1[g_2]) + (1-p) s_{S2}(1 - g_2) & p b_1 + (1-p) b_2 \\ (p s_{S1} s_{Y1} g_1[g_2] + (1-p) s_{S2} s_{Y2} g_2)\, comp[A[t]] & p s_{A1} + (1-p) s_{A2} \end{pmatrix}. \qquad (10)$$

We then conducted an evolutionary invasion analysis, in which a resident population was allowed to reach an equilibrium size (assuming this to be stable) and then the invasion ability of a mutant with a different germination rate was evaluated, as measured by the leading eigenvalue of $\mathbf{T_C}$ for a rare mutant (details in Appendix S2). If germination rates affect the number of seedlings but not the nature of competition (i.e. $comp[A[t]]$ is not a function of g_1 or g_2), the results remain the same as above (for mechanisms 1 and 2), but with birth rates now multiplied by $comp[A[t]]$.

Mechanism 3: Effects of synchronization with disturbances

Here, we focus on a particular type of temporal variation in environment, such as large-scale disturbances like fire, which affect adult survival and potentially germination rates across the entire population at the same time. Synchronizing germination to occur immediately after a disturbance then maximizes the number of years as an adult before experiencing the next disturbance. By contrast, plants that germinate in nondisturbance years (i) have fewer chances to produce seeds before experiencing a disturbance and (ii) are more likely to die in a disturbance before producing seeds at all. We show that these costs of poor synchronization can be strong enough to cause plants to forgo germination in years without disturbances, even in the absence of differential seedling survival or trade-offs.

In this section, the notation for environment 1 ($i = 1$) is used for years with population-scale disturbances and environment 2 ($i = 2$) specifies life-history parameters in nondisturbance years. We assume that the population census is such that germination rate in disturbance years (disturbance-induced germination rate, g_1) is measured after the disturbance (so that it can be affected by disturbances). With fire, for example, fire years ($i = 1$) would be associated with low adult survival (s_{A1}) but potentially high seedling survival (s_{Y1}) because seeds emerging after the fire experience a low competition and high nutrient environment.

The transition matrices describing changes in seed and adult population sizes in disturbance and nondisturbance years are as follows:

$$\mathbf{T_1} = \begin{pmatrix} s_{S1}(1-g_1) & b_1 \\ s_{S1}s_{Y1}g_1 & s_{A1} \end{pmatrix}, \tag{11a}$$

$$\mathbf{T_2} = \begin{pmatrix} s_{S2}(1-g_2) & b_2 \\ s_{S2}s_{Y2}g_2 & s_{A2} \end{pmatrix}. \tag{11b}$$

Firstly, we consider a disturbance cycle, in which disturbances occur every τ years. That is, we include a disturbance year followed by a number of nondisturbance years ($\tau-1$). To describe population size changes over the entire cycle, we apply the disturbance year transition matrix ($\mathbf{T_1}$) and then iterate the transition matrix $\tau-1$ times for nondisturbance years ($\mathbf{T_2}$). Using standard rules of matrix algebra,

$$\mathbf{T_2}^{\tau-1} \cdot \mathbf{T_1} = \mathbf{A} \cdot \mathbf{D}^{\tau-1} \cdot \mathbf{A}^{-1} \cdot \mathbf{T_1} \tag{12}$$

where **A** is a matrix in which the columns are the eigenvectors of $\mathbf{T_2}$ and **D** is a matrix in which the diagonal elements are the eigenvalues of $\mathbf{T_2}$.

The logic of our analysis is similar to above. We evaluate whether modifying the germination parameters increases or decreases the long-term growth rate, λ, given by the leading eigenvalue of the entire cycle matrix (equation 12). We provide the details of our approach in Appendix S3.

Although (12) accurately describes changes in the long-term growth rate over the entire cycle, it is quite complex to analyse. We thus used an approximation to simplify the analysis. Specifically, we assume that **D** can be approximated by omitting the smaller eigenvalue. This approximation is most accurate when the difference between eigenvalues is large and/or when the number of years between disturbances is large (over time, the effects of the larger eigenvalue dominate, e.g. Otto & Day, 2007, box 9.1). Care must therefore be taken in interpreting the results when the cycle length is short, which is also when we find that conditional germination strategies tend to be favoured. Thus, this approximation only serves as a guide to conditions that favour conditional germination; the accuracy of the approximation is discussed in Appendix S3.

To distinguish synchronization effects from those already explored, we focus on the case where there are no direct trade-offs between germination rates (g_1 and g_2) and where seedling survival rates in disturbance and nondisturbance environments are equal ($s_{Y1} = s_{Y2}$). We found that mutants with higher disturbance-induced germination rates (g_1) are expected to have higher long-term growth rates, given that the population is able to grow in normal years (as assumed throughout this section). We therefore assumed that disturbance-induced germination rate is high ($g_1 = 1$) when analysing the evolution of the germination rate in nondisturbance years, g_2. For very long disturbance cycles (high τ), higher germination rates in nondisturbance years should also give higher long-term growth rates. However, when the disturbance cycle is short enough (less than the critical value τ_c, see equation A.46), conditional germination, $g_2 < 1$, is favoured.

We took the derivative of τ_c with respect to life-history parameters in the disturbance year to see the effect that the parameters have on the length of the disturbance cycles over which conditional germination is expected to evolve. We found that increasing seed bank persistence through disturbances (s_{S1}) and increasing disturbance-induced germination (g_1) increases the parameter space over which selection favours conditional germination

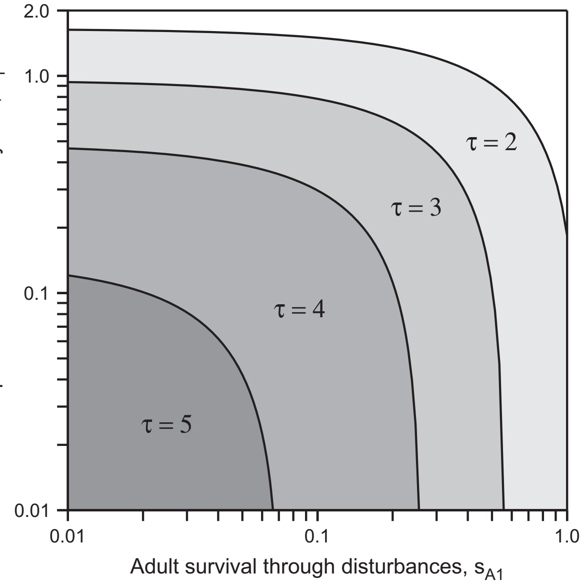

Fig. 3 The parameters for which conditional germination is expected to evolve for various different disturbance cycle lengths (τ) based on our approximation, assuming adults reach reproductive maturity immediately (in the time step after germination). See Fig. S2 for comparison with a nonapproximated model. Increasingly dark grey areas indicate where the germination rate in nondisturbance years (g_2) is expected to evolve below one (conditional germination) for cycle lengths of 2, 3, 4 and 5 (lighter regions overlap darker regions). In the white region, conditional germination is not expected to evolve for any cycle length, τ. Other parameters are $g_1 = 1$, $s_{Y1} = s_{Y2} = 0.6$, $s_{S1} = s_{S2} = 0.9$, $b_2 = 2$ and $s_{A2} = 0.7$.

strategies. However, increasing seeds produced in the disturbance year (b_1) and adult survival through disturbances (s_{A1}) decreases the range of disturbance intervals for which conditional germination should evolve.

Our results indicate that conditional germination ($g_2 < 1$) should evolve when adults that germinate in nondisturbance years risk death in a disturbance before producing a significant number of seeds. By contrast, conditional germination should not generally evolve when disturbances have little effect on adult survival (s_{A1} is high) and when adults are guaranteed to produce a large number of seeds even if they mature for the first time in the disturbance year (b_1 is high), see Fig. 3.

Figure 3 suggests that conditional germination should only evolve for relatively short disturbance cycles. However, in the above models, organisms become reproductively mature after 1 year and so the advantages of synchronization are necessarily weak. We expand on these analytical results using some numerical simulations that include more complex demography.

We based our simulations on those of Enright *et al.* (1998), using parameters that approximately correspond to the demography of *B. hookeriana*, an Australian shrub in the Proeaceae that retains almost all seeds on the plant until immediately after a fire. The parameters are given in Table 1. The major technical difference between our simulations and those of Enright *et al.* (1998) is that we assume seeds remain in the seed bank after plant death, whereas seeds died with the parent (but not in fires) in the original model. This change allowed us to simulate the entire population by multiplying by the appropriate matrix in (11) rather than tracking individuals. We also allow a small fraction of adults to escape disturbances in microclimates (s_{A1} = 0.005); this prevents complete population extinction if ever two disturbance events occur in a row. We made two important biological modifications to expand on our analytical results: (i) we varied the number of years before maturity is reached to show that conditional germination should only evolve when there is a significant risk of death before producing seeds, (ii) we explored nonperiodic disturbances (fires in this model) to show that the 'synchronization effect' continues to favour conditional germination. In all our simulations, there is no difference in seedling survival between environments ($s_{Y1} = s_{Y2}$, mechanism 1 absent).

For particular fixed disturbance (fire) cycle lengths, we varied the number of years to first reproduction ($A2$), from 1 to 3 to 5 years and recorded the optimal germination rate in normal years (the g_2 that yielded the highest long-term growth rate, λ). The results are plotted in Fig. 4, which shows that the advantage of conditional germination is increased when the number of years to reproductive maturity is increased. This demonstrates that 'synchronization advantages' favour conditional germination in this model, which was not originally made explicit in Enright *et al.* (1998).

For variable disturbance cycles, we next drew integer disturbance intervals from a Weibull distribution, see

Table 1 Default parameters used in numerical simulations.

Parameter	Symbol	Default value
Fire-induced germination rate	g_1	1
Normal germination rate	g_2	0–1*
Seed survival	$s_{S2} = s_{S1}$	0.94
Adult survival	s_{A2}	*p*[*age*]†
Adult survival (fire)	s_{A1}	0.005
Seedling survival	$s_{Y1} = s_{Y2}$	0.042
Seed production	$b_2 = b_1$	*m*[*age*]‡
Age at first reproduction	$A2$	5
Age at max reproduction	$A3$	15
Max seed age	Vm	15
Max adult age	$A4$	40

*Varied between 0 and 1 in steps of 0.05, the value yielding the highest long-term growth rate (λ, leading eigenvalue of the transition matrix) was recorded.

†For $1 < age < 25$, $p[age] = (1/f[age])/(1/f[age-1])$ where $f[age] = 69.03 \log_{10}[age] + 23.60$. For $25 \le age$, $p[age] = (1/f[age])/(1/f[age-1])(1-0.01(age-24))$.

‡For $age < A2$, $m[age] = 0$. $m[age] = 200$ when $A3 \le age$. For $A2 \le age < A3$, $m[age] = \frac{200(age+1-A2)}{1+A3-A2}$.

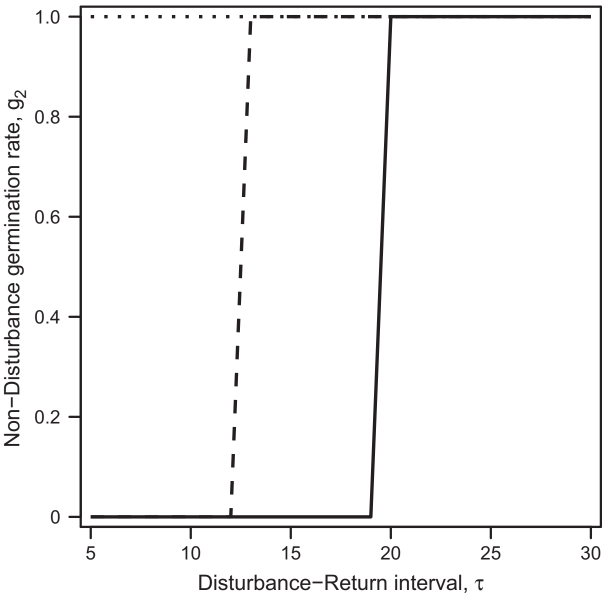

Fig. 4 The germination rate in nondisturbance (fire) years (g_2) that yields the highest long-term growth rate in our numerical analysis of a life history akin to *Banksia hookeriana* (Enright *et al.*, 1998) for different disturbance-return intervals. The solid line is for the default parameters with an age of reproductive maturity of 5 years, whereas the dashed and dotted lines are where age at first reproduction ($A2$) was reduced to 3 and 1 years, respectively. Notice that when adults become reproductively mature immediately environment-dependent germination never evolves (dotted line).

Fig. 5a. We varied the regularity of disturbances by using a shape parameter (β) of 1, 2 or 4, which represent increasing regularity of disturbances, starting from the exponential distribution ($\beta = 1$, constant disturbance risk, $\beta = \infty$ corresponds to the periodic case considered above). In Fig. 5b, we plotted the germination strategy in nonfire years that gave the highest growth rate (averaged across replicate 100 draws of 20 disturbances) for various mean disturbance intervals. Figure 5b shows that, even when disturbance intervals are highly variable ($\beta = 1$), conditional germination (low g_2) can be advantageous. We also note from Fig. 5b that variability tends to favour mixed strategies, with g_2 values between zero and one, representing bet hedging between the long and short intervals.

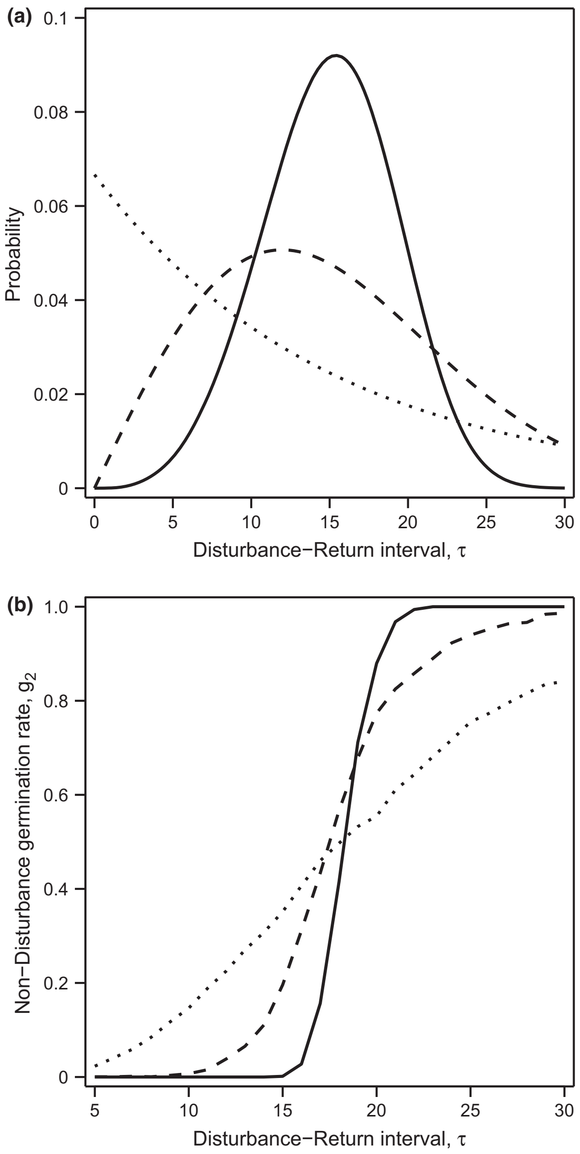

Fig. 5 The effect of variability in disturbance-return interval on the evolution of conditional germination. (a) The shape parameter affects the Weibull distribution used for the fire-return interval (τ). The mean in each case is 15 years between disturbances. The dotted line shows the probability of selecting disturbance-return intervals when the Weibull shape parameter (β) is 1 and is equivalent to an exponential distribution with expected value 15. The dashed and solid lines are for $\beta = 2$ and 4, respectively, and represent increasing regularity due to an increasing hazard with time since the last disturbance. (b) The solid, dashed and dotted lines show the corresponding average germination rate in nondisturbance years (g_2) that yielded the highest long-term growth rate in our simulations. Here the x-axis represents the mean disturbance-return interval.

Discussion

In this paper, we explored three mechanisms by which a developmental delay (e.g. seed dormancy) can be favoured in certain environments but not in others. This work builds upon the model of annual plants developed by Cohen (1967) but allows for demographic structure. Although Cohen predicted that optimal germination strategies would match the yields from any one environment, demographic structure complicates the picture because yield must be calculated over multiple time steps and hence over multiple environments. We identified three mechanisms by which a developmental delay triggered by the state of the environment (conditional germination) can evolve.

Mechanism 1: If seedling survival is sufficiently low in 'bad' environments, it is optimal to limit germination to 'good' patches. In desert plants, seedling survival is much higher in years with high rainfall, and germination rates are correspondingly higher when early season rainfall is high (Evans *et al.*, 2007). Similarly, 'classical disturbances' (White & Pickett, 1985), such as fires, create discrete patches in which resources are higher due to decreased biological use, an ash-bed effect (Serrasolses & Vallejo, 1999; Pausas *et al.*, 2003) and/or increased decomposition. For nonannuals, only the extreme case in which seedling survival is impossible in 'bad' environments has been formally considered (in the context of post-fire germination responses, Lamont *et al.*, 1991). Empirically, the establishment ability of seeds germinating in post-fire environments is not always elevated, and establishment in other years is often not negligible (e.g. O'Dowd & Gill, 1984; Cowling & Lamont, 1987; Brewer, 1999; Quintana-Ascencio & Menges, 2000; Liu *et al.*, 2005). As Bond & Wilgen (1996, p142) point out, it was not previously obvious whether reported differences in seedling survival are large enough to select against germination in 'bad' years.

We used a simple model lacking trade-offs and temporal variation to find a threshold level of seedling survival in 'bad' patches below which conditional germination is expected to be advantageous. The conditions for conditional germination to evolve via this mechanism are broader when 'good' environments are common, seed survival is high, adult survival is low, and seed production is low. These results can thus guide empirical work to determine whether demographic parameters would or would not favour conditional germination in a particular species.

In the first two sections (low seedling survival and trade-offs), we used the simplifying assumption that a random proportion of the (many) patches experience each environment in each time step, with no reference to the previous environments experienced. Thus, after germination and seedling survival occurs in a particular environment, there is no link between the environment experienced at the time of germination and the subsequent environments experienced by adults. We predict that, in a spatially explicit model where the environment experienced across the life span depends on the environment at the time of germination, low adult survival and fecundity (not just low seedling survival) in 'bad' environments could also favour conditional germination, assuming seeds can experience different environments by delaying germination.

We also incorporated intraspecific competition affecting seedling survival and found that our results were quantitatively altered but qualitatively unaffected. Similarly, the density-independent annual plant model by Cohen (1966) was extended to include density dependence by Bulmer (1984), Ellner (1985a) and Ellner (1985b). In these annual plant models with temporal environmental variation, density dependence can exacerbate the effect of environmental variation on germination fraction (or create temporal variation via deterministic dynamics, Ellner, 1987). In addition, we note that annual plant models show that spatial structure can introduce sibling competition, which can reduce the optimal germination fraction (Ellner, 1987). Gremer & Venable (2014) find that annual plant models with density dependence included predict germination fractions more accurately than density-independent models. We caution that our model of competition was highly idealized to make analytical headway. Although density-dependent competition was experienced equally everywhere in our model, competition should be lessened in patches that have recently experienced low adult survival. A more appropriate but complex model would be spatially explicit with differences in seedling survival affected by competitive interactions only within the same patch.

Mechanism 2: Trade-offs can make it difficult to germinate equally well in all environments, making conditional germination more likely to evolve. We considered a direct physical or developmental trade-off between germination rates, such that a plant would have to decrease germination rate in environment 1 to increase the germination rate in environment 2. This trade-off is over-and-above the fact that seeds that germinate in one environment are unavailable to germinate in the future, which can also be seen as a form of trade-off that underlies all models of delayed development.

Trade-offs are likely to arise whenever the features that protect seeds from the environment also alter their ability to germinate. For example, thickened seed coats or retention in cones may prevent germination in most environments but allow seeds to survive fires and thus allow increased germination in a post-fire environment. Indeed, many species with temperature-induced germination produce a mixture of seeds that are specialized for either post-fire or for interfire germination (Keeley, 1995). This suggests that individual seeds cannot do both well, which will generate a trade-off if the total number of seeds is limited. Previously, Tonnabel *et al.* (2012) considered a trade-off between seed production and maintenance (b and s_S here). They assume seedling survival in 'bad' environments is negligible so that selection should maximize germination in 'good' (post-fire) environments only, which occurs at an intermediate (mixed) strategy with their trade-off.

To demonstrate the effects of trade-offs on conditional germination, we considered a direct trade-off between germination rates, which has not been explored before. We show that, with convex trade-off shapes (dashed line in Fig. 2), specialized germination strategies are favoured, even for parameters that did not favour conditional germination in the model without trade-offs. By contrast, concave trade-offs (solid line in Fig. 2) can favour a mixed strategy with some germination in both environments, which maximizes reproductive opportunities across all patches. Thus, intermediate germination rates can be favoured due to trade-offs, in addition to bet hedging caused by temporal environmental variation (see next section).

Mechanism 3: Limiting germination to disturbance events minimizes the risk of experiencing another disturbance before reproducing. The timing of insect diapause is thought to depend on the risk of seasonal disturbances (e.g. frost or drought) occurring before reproductive maturation is reached (Cohen, 1970; Taylor, 1980; Hairston & Munns, 1984; Taylor & Spalding, 1989; Bradford & Roff, 1993; Spencer & Colegrave, 2001). We explored similar risks in a model where germination strategy depends on environmental state rather than time. We showed that conditional germination is more likely to evolve when plants are prone to population-scale disturbances, promoting life-histories that are more synchronized with these disturbances. As in our first model, conditional germination is more likely to evolve by this mechanism when seeds survive disturbances well but adults do not.

Our analytical results indicate that conditional germination should only evolve if severe (detrimental to adult survival) disturbances can occur before a significant number of offspring are produced (Fig. 3). In particular, organisms that take multiple years to reach reproductive maturity should have an increased risk of dying during disturbances before reproducing. A previous model with prereproductive age classes by Enright *et al.* (1998) suggested that conditional germination strategies have higher long-term growth rates even without differences in seedling survival but the mechanism favouring conditional germination was not discussed or made explicit. We produced a model based on that of Enright *et al.* (1998) but reduced the number of years until reproductive maturity to show that this eliminates the benefits of conditional germination (Fig. 4). To our knowledge, avoiding death before reaching reproductive maturity has not previously been theoretically investigated as an important driver for the evolution of conditional germination strategies, most likely because it requires a relatively complex demographic model with environment-dependent germination.

Interestingly, a synchronization advantage continues to favour conditional germination strategies even when the period between disturbances is variable. In this case, incomplete rather than complete disturbance-dependent germination strategies often have the highest long-term growth rate because they bet hedge (Philippi & Seger, 1989) between experiencing long and short intervals. This is an example of 'germ banking', as defined by Evans & Dennehy (2005), where unpredictable environmental variation favours an intermediate strategy. Figure 5 shows that, even when the disturbance probability is exactly the same in each year ($\beta = 1$, exponentially distributed disturbance intervals) and there is no difference in seedling survival, conditional germination is expected to evolve when plants take multiple years to reach reproductive maturity. Demonstrating this case explicitly is significant because many types of disturbance are likely to be nonperiodic ($\beta = 1$). For fires, a Weibull shape parameter of around 2 (see Fig. 5a) has been estimated in some ecosystems (Polakow & Dunne, 1999; Moritz *et al.*, 2008). Fire hazard is thought to increase with years since a fire due to vegetation build up (Baeza *et al.*, 2002; De Luís *et al.*, 2004), causing a negative autocorrelation in fire intervals (Dodson *et al.*, 2005) and making fires more uniformly spread over time (as in our periodic model). On the other hand, a positive temporal autocorrelation between disturbances (clumping, e.g. due to climate phenomena) would reduce the efficacy of the synchronization mechanism because disturbance risk is increased in the years following a disturbance.

In this paper, we determine the conditions under which these three mechanisms allow the evolution of environment-dependent germination. We first explored the most commonly envisioned mechanism (mechanism 1, low seedling survival in 'bad' environments) and then show that trade-offs and synchronization effects (mechanisms 2 and 3) can favour environment-dependent germination even when there is no difference in seedling survival. These models provide a framework for exploring which mechanisms might be responsible for conditional germination in empirical systems. For example, we have shown that the fact that it takes several years for the Australian shrub *B. hookeriana* to mature greatly facilitates the evolution of environment-dependent germination in this system (Fig. 4). Thus, by obtaining the required demographic parameters and using the models to determine what conditions favour conditional germination, future empirical work promises to inform us why some species wait for particular environments to continue development.

Acknowledgments

We thank Fernando Ojeda for his inspiration and input. We also thank Florence Débarre, Jasmine Ono, Matthew Osmond, Michael Doebeli, Carl Rothfels and four anonymous reviewers for their comments. Funding for this project was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), the University of British Columbia (UBC), and an NSERC-CREATE Training Program in Biodiversity Research (BRITE).

References

Baeza, M.J., De Luís, M., Raventos, J. & Escarré, A. 2002. Factors influencing fire behaviour in shrublands of different stand ages and the implications for using prescribed burning to reduce wildfire risk. *J. Environ. Manage.* **65**: 199–208.

Baskin, C.C. & Baskin, J.M. 2014. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd edn. Academic Press, London.

Bond, W.J. & Wilgen, B.W. 1996. *Fire and Plants*. Chapman & Hall, London.

Bradford, M.J. & Roff, D.A. 1993. Bet hedging and the diapause strategies of the cricket *Allonemobius fasciatus*. *Ecology* **74**: 1129–1135.

Bradshaw, S.D., Dixon, K.W., Hopper, S.D., Lambers, H. & Turner, S.R. 2011. Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends Plant Sci.* **16**: 69–76.

Brewer, J.S. 1999. Short-term effects of fire and competition on growth and plasticity of the yellow pitcher plant, *Sarracenia alata* (Sarraceniaceae). *Am. J. Bot.* **86**: 1264–1271.

Bulmer, M.G. 1984. Delayed germination of seeds: Cohen's model revisited. *Theor. Popul. Biol.* **23**: 367–377.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* **12**: 119–129.

Cohen, D. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *J. Theor. Biol.* **16**: 1–14.

Cohen, D. 1970. A theoretical model for the optimal timing of diapause. *Am. Nat.* **104**: 389–400.

Cohen, D. & Levin, S.A. 1987. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In: *Proceedings of International Symposium on Mathematical Biology* (E. Teramoto & M. Yamaguti, eds), pp. 110–122. Springer Verlag, Berlin.

Cowling, R.M. & Lamont, B.B. 1987. Post-fire recruitment of four co-occurring Banksia species. *J. Appl. Ecol.* **24**: 645–658.

De Luís, M., Baeza, M.J., Raventós, J. & González-Hidalgo, J.C. 2004. Fuel characteristics and fire behaviour in mature Mediterranean gorse shrublands. *Int. J. Wildl. Fire* **13**: 79.

Dodson, J.R., Robinson, M. & Tardy, C. 2005. Two fine-resolution Pliocene charcoal records and their bearing on pre-human fire frequency in south-western Australia. *Austral. Ecol.* **30**: 592–599.

Ellner, S. 1985a. ESS germination strategies in randomly varying environments. I. Logistic-type models. *Theor. Popul. Biol.* **28**: 50–79.

Ellner, S. 1985b. ESS germination strategies in randomly varying environments. II. Reciprocal Yield-Law models. *Theor. Popul. Biol.* **28**: 80–116.

Ellner, S. 1987. Competition and dormancy: a reanalysis and review. *Am. Nat.* **130**: 798–803.

Enright, N.J., Marsula, R., Lamont, B.B. & Wissel, C. 1998. The ecological significance of canopy seed storage in fire-prone environments: a model for nonsprouting shrubs. *J. Ecol.* **86**: 946–959.

Evans, M.E.K. & Dennehy, J.J. 2005. Germ banking: bet-hedging and variable release from egg and seed dormancy. *Q. Rev. Biol.* **80**: 431–451.

Evans, M.E.K., Ferriére, R., Kane, M.J. & Venable, D.L. 2007. Bet hedging via seed banking in desert evening primroses (Oenothera, Onagraceae): demographic evidence from natural populations. *Am. Nat.* **169**: 184–194.

Gremer, J.R. & Venable, D.L. 2014. Bet hedging in desert winter annual plants: optimal germination strategies in a variable environment. *Ecol. Lett.* **17**: 380–387.

Gremer, J.R., Crone, E.E. & Lesica, P. 2012. Are dormant plants hedging their bets? Demographic consequences of prolonged dormancy in variable environments. *Am. Nat.* **179**: 315–327.

Hairston, N.G. Jr & Munns, W.R. Jr 1984. The timing of copepod diapause as an evolutionarily stable strategy. *Am. Nat.* **123**: 733–751.

Keeley, J.E. 1995. Seed-germination patterns in fire-prone mediterranean-climate regions. In: *Ecology and biogeography of Mediterranean Ecosystems in Chile, California and Australia* (M.T. Arroyo, P.H. Zedley & M.D. Fox, eds), pp. 239–273. Springer Verlag, New York, NY.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* **16**: 406–411.

Klinkhamer, P.G.L., de Jong, T.J., Metz, J.A.J. & Val, J. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theor. Popul. Biol.* **32**: 127–156.

Koons, D.N., Metcalf, C.J.E. & Tuljapurkar, S. 2008. Evolution of delayed reproduction in uncertain environments: a life history perspective. *Am. Nat.* **172**: 797–805.

Lamont, B.B. & Enright, N.J. 2000. Adaptive advantages of aerial seed banks. *Plant Species Biol.* **15**: 157–166.

Lamont, B.B., Le Maitre, D.C., Cowling, R.M. & Enright, N.J. 1991. Canopy seed storage in woody plants. *Bot. Rev.* **57**: 277–317.

Levin, S.A., Cohen, D. & Hastings, A. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* **26**: 165–191.

Liu, H., Menges, E.S. & Quintana-Ascencio, P.F. 2005. Population viability analyses of *Chamaecrista keyensis*: effects of fire season and frequency. *Ecol. Appl.* **15**: 210–221.

MacArthur, R.H. 1972. *Geographical Ecology*. Princeton University Press, Princeton, NJ.

Midgley, J. 2000. What are the relative costs, limits and correlates of increased degree of serotiny? *Austral. Ecol.* **25**: 65–68.

Moritz, M.A., Moody, T.J., Miles, L.J., Smith, M.M. & Valpine, P. 2008. The fire frequency analysis branch of the pyrostatistics tree: sampling decisions and censoring in fire interval data. *Environ. Ecol. Stat.* **16**: 271–289.

O'Dowd, D.J. & Gill, A.M. 1984. Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. *Ecology* **65**: 1052–1066.

Otto, S.P. & Day, T. 2007. *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University Press, Princeton, NJ.

Pake, C.E. & Venable, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* **77**: 1427–1435.

Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T. & Vallejo, R. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. *Plant. Ecol.* **169**: 205–213.

Perkins, D.D. & Turner, B.C. 1988. Neurospora from natural populations: toward the population biology of a haploid eukaryote. *Exp. Mycol.* **12**: 91–131.

Philippi, T. & Seger, J. 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**: 41–44.

Polakow, D.A. & Dunne, T.T. 1999. Modelling fire-return interval T: stochasticity and censoring in the two-parameter Weibull model. *Ecol. Modell.* **121**: 79–102.

Quintana-Ascencio, P.F. & Menges, E.S. 2000. Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. *Am. J. Bot.* **87**: 690–699.

Rees, M. 1996. Evolutionary ecology of seed dormancy and seed size. *Philos. Trans. R. Soc. B: Biol. Sci.* **351**: 1299–1308.

Roerdink, J.B.T.M. 1988. The biennial life strategy in a random environment. *J. Math. Biol.* **26**: 199–215.

Roerdink, J.B.T.M. 1989. The biennial life strategy in a random environment. *J. Math. Biol.* **27**: 309–319.

Serrasolses, I. & Vallejo, V.R. 1999. Soil fertility after fire and clear-cutting. In: *Ecology of Mediterranean Evergreen Oak Forests* (F. Rodá, J. Retana, C.A. Gracia & J. Bellot, eds), pp. 315–328. Springer Verlag, New York, NY.

Simons, A.M. 2014. Playing smart vs. playing safe: the joint expression of phenotypic plasticity and potential bet hedging across and within thermal environments. *J. Evol. Biol.* **27**: 1047–1056.

Spencer, M. & Colegrave, N. 2001. Hatching fraction and timing of resting stage production in seasonal environments: effects of density dependence and uncertain season length. *J. Evol. Biol.* **14**: 357–367.

Taylor, F. 1980. Optimal switching to diapause in relation to the onset of winter. *Theor. Popul. Biol.* **18**: 125–133.

Taylor, F. & Spalding, J.B. 1989. Timing of diapause in relation to temporally variable catastrophes. *J. Evol. Biol.* **2**: 285–297.

Tonnabel, J., Van Dooren, T.J., Midgley, J., Haccou, P., Mignot, A., Ronce, O. *et al.* 2012. Optimal resource allocation in a serotinous nonresprouting plant species under different fire regimes. *J. Ecol.* **100**: 1464–1474.

Tuljapurkar, S. 1990. Delayed reproduction and fitness in variable environments. *Proc. Natl. Acad. Sci. USA* **87**: 1139–1143.

Tuljapurkar, S. & Istock, C. 1993. Environmental uncertainty and variable diapause. *Theor. Popul. Biol.* **43**: 251–280.

Tuljapurkar, S. & Wiener, P. 2000. Escape in time: stay young or age gracefully? *Ecol. Modell.* **133**: 143–159.

Venable, D.L. 2007. Bet hedging in a guild of desert annuals. *Ecology* **88**: 1086–1090.

Venable, D.L. & Lawlor, L. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* **46**: 272–282.

White, P.S. & Pickett, S.T. 1985. Introduction. In: *The Ecology of Natural Disturbance and Patch Dynamics* (S.T. Pickett, ed.), pp. 1–16. Academic Press Inc., Orlando, FL.

Wiener, P. & Tuljapurkar, S. 1994. Migration in variable environments: exploring life-history evolution using structured population models. *J. Theor. Biol.* **166**: 75–90.

Wilbur, H.M. & Rudolf, V.H.W. 2006. Life history evolution in uncertain environments: bet hedging in time. *Am. Nat.* **168**: 398–411.

Wolfram Research Inc. 2010. *Mathematica, Version 8.0 edn*. Wolfram Research, Inc., Champaign, Illinois.

Supporting information

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

Figure S1 An example of a discrepancy between the approximated transition matrix across a disturbance cycle $\tilde{\mathbf{T}}_{\text{cycle}}$ and the full matrix.

Figure S2 A version of Figure 3 that is drawn using the non-approximated transition matrix $\mathbf{T}_{\text{cycle}}$.

Data S1 Supplementary Mathematica file.

Appendix S1 Differences in seedling survival.

Appendix S2 Trade-offs.

Appendix S3 Approximating the cycle matrix.

Received 1 May 2014; revised 31 July 2014; accepted 12 August 2014