Seed Dormancy and Delayed Flowering in Monocarpic Plants: Selective Interactions in a Stochastic Environment

Mark Rees,1,* Dylan Z. Childs,1† Jessica C. Metcalf,2‡ Karen E. Rose,1§ Andy W. Sheppard,3, and Peter J. Grubb4#

1. Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; 2. Max Planck Institute for Demographic Research, Konrad-Zuse-Straße 1, 18057 Rostock, Germany; 3. Commonwealth Scientific and Industrial Research Organization (CSIRO) Entomology/Cooperative Research Centre for Weed Management Systems, CSIRO European Laboratory, Campus International de Baillarguet, 34980 Montferrier-sur-Lez, France; 4. Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, United Kingdom

Submitted August 10, 2005; Accepted April 4, 2006; Electronically published July 10, 2006

ABSTRACT: We explore the effects of temporal variation in multiple demographic rates on the joint evolution of delayed reproduction and seed dormancy using integral projection models (IPMs). To do this, we extend the standard IPM to include a discrete state variable representing the number of seeds in the seed bank, density-dependent recruitment, and temporal variation in demography. Parameter estimates for Carlina vulgaris and Carduus nutans are obtained from long-term studies. Carlina is relatively long lived and has a short-lived seed bank, whereas most Carduus plants flower in their first year and the seed bank is long lived. Using the evolutionarily stable strategy (ESS) approach, we predict the observed flowering and germination strategies. There is excellent agreement between the predictions and the field observations. The effects of temporal variation on the joint ESS are partitioned into components arising from nonlinear averaging (systematic changes in the mean resulting from the interaction between variability and nonlinearity) and nonequilibrium dynamics (fluctuations in fitness caused by temporal variation). This shows that temporal variation can have substantial effects on the observed flowering and germination strategies and that covariance between demographic processes is important. We extend the models to include spatial population structure and assess the robustness of the results from the nonspatial models.

Keywords: integral projection model, Carlina vulgaris, Carduus nutans, evolutionarily stable strategy (ESS), nonlinear averaging, nonequilibrium dynamics.

Reproductive delays are a ubiquitous feature of plant and animal life cycles and of explaining why organisms defer reproduction, a classic problem in evolutionary biology (Cole 1954). In plants, reproductive delays can be usefully divided into pre- and postestablishment delays. These differ fundamentally because postestablishment delays, such as delayed reproduction, can increase fecundity as a result of growth, whereas this is not possible for preestablishment delays, such as seed dormancy. To explain the adaptive significance of postestablishment delays, evolutionary biologists have traditionally focused on the relative costs (mortality) and benefits (increased fecundity). In contrast, for preestablishment delays, because there is no growth, adaptive explanations have focused on bet hedging, exploring, for example, the evolution of seed dormancy in response to temporal fluctuations in fitness (Cohen 1966).

However, despite their differences, pre- and postestablishment delays can have similar population dynamic effects (Tuljapurkar and Wiener 2000). For example, both delayed size-dependent reproduction and seed dormancy result in reproduction within a cohort being spread through time as a result of individuals reaching the critical size for flowering or seeds germinating in different years (Cohen 1966; Klinkhamer and de Jong 1983; Roerdink 1988). Thus, both traits allow bet hedging, leading to the expectation that there will be selective interactions between them. In general, theory predicts that life-history attributes that reduce the impact of environmental variation on fitness will show patterns of negative covariation ( Venom and Brown 1988; Rees 1994). For example, Rees (1994) explored the evolution of dormancy in perennial plant populations and showed that the presence of long-lived adults buffered the population from temporal variation, leading to selection for less seed dormancy.
In monocarpic perennial plants, in which reproduction is fatal, both delayed reproduction and seed dormancy provide mechanisms for reducing the effects of temporal variation in reproductive success (Cohen 1966; Klinkhamer and de Jong 1983; Roerdink 1988). This leads to the idea that there are two extreme life histories in monocarpic perennials, those where persistence is primarily dependent on the rosette bank and those that rely on a seed bank (Kachi 1990). Whether it is advantageous to form a rosette or a seed bank will clearly depend on the relative mortality rates of seeds and established plants and the growth rate of established plants. Interestingly, even when the costs of forming a seed bank or rosette bank are equal and there is no growth of rosettes, selection tends to be self-reinforcing, leading to life cycles with a single delay (Tulipapurkar and Wiener 2000). Species that form a rosette bank and have little or no seed bank include Carlina vulgaris, Ipomopsis aggregata, Lactuca virosa, and Oenothera glazioviana, whereas species such as Carduus nutans and Oenothera biennis have relatively short-lived rosettes and long-lived seed banks (Boorman and Fuller 1984; Kachi and Hirose 1985; Kachi 1990; Popay and Medd 1990; Campbell 1997; de Jong et al. 2000).

Temporal variation can influence fitness in at least two distinct ways: through changes in the mean demographic rates or through fluctuations in fitness caused by variance in demographic rates (Gillespie 1977; Frank and Slatkin 1990; Real and Ellner 1992; Houston and McNamara 1999). This latter effect is a result of fluctuating selection and the payoff from a particular action depending on population structure, which itself fluctuates as a result of variance in demographic rates (Rees et al. 2004). The nature of the temporal fluctuations in demographic rates is also important (Childs et al. 2004; Rees et al. 2004). In the case of temporal variation in recruitment, which is demographically equivalent to variation in reproductive success, selection favors larger sizes at flowering. This is because large flowering size, coupled with variable growth, distributes reproduction over several years, thereby mitigating the effects of low-recruitment years. Again, this leads to the prediction that species that spread reproduction over several years should have less dormancy. In contrast, the fluctuations in fitness generated by temporal variation in growth and survival select for smaller sizes at flowering (Rees et al. 2004) because this reduces the chance that an individual will be exposed to a low survival or growth year. This leads to the opposite prediction because species with greater seed dormancy can potentially have riskier flowering strategies and so flower larger. Testing theories based on temporal variation is therefore difficult because one has to quantify not only average demographic rates but also their variances and possibly covariances and separate the effects of changes in mean demographic rates from changes in their variance. This difficulty means that there are few attempts to test the theory directly, and instead studies have concentrated on comparative analyses exploring the predicted patterns of covariation (Mazer 1989; Rees 1993, 1996; Leishman and Westoby 1994; Thompson et al. 2002).

To test these ideas, we explored the joint evolution of size-dependent flowering and seed dormancy by using the recently introduced integral projection model (IPM; Easterling et al. 2000; Rees and Rose 2002; Childs et al. 2003, 2004; Rose et al. 2005; Ellner and Rees 2006b). We first extend this approach to include a seed bank and temporal variation in the environment. The population biology of C. vulgaris and C. nutans is then briefly summarized and parameter estimates for the models obtained. The joint evolution of delayed reproduction and seed dormancy is then explored using the evolutionarily stable strategy (ESS) approach. We partition the effects of temporal fluctuation in growth, survival, and recruitment into components associated with nonlinear averaging and nonequilibrium dynamics (Rees et al. 2004). This partitioning was done by randomizing the order of the yearly parameters so the effects of covariance between different sources of temporal fluctuation can be isolated. The influence of temporal variation on fitness depends on the spatial scale over which variation acts and on dispersal (Bulmer 1984). We therefore extend the models to include spatial structure and use these models to assess the robustness of the conclusions from the simpler nonspatial models.

Material and Methods

The IPM describes how a continuously size-structured population changes in discrete time (Easterling et al. 2000). The state of the population is described by a distribution function, \( n(x, t) \), where \( n(x, t)dx \) is the number of individuals with size in the range \( [x, x + dx] \). The dynamics are then

\[
n(y, t + 1) = \int_{\Omega} [p(y, x) + f(y, x)] n(x, t) dx
\]

\[
= \int_{\Omega} k(y, x) n(x, t) dx,
\]

where \( k(y, x) \), known as the kernel, describes all possible transitions from size \( x \) to size \( y \), including births, and \( \Omega \) is the set of all possible sizes. The kernel is composed of two parts describing the production of size \( y \) offspring by size \( x \) parents, \( f(y, x) \), and the movement of individuals from size \( x \) to size \( y \), \( p(y, x) \). To extend the model to include a seed bank, we first define the seed production function,
f(x), so that the fecundity function, f(y, x), can be written as \( f_y(x) f(x) \), where \( f_y(x) \) is the probability density function of recruit sizes. The seed production function, f(x), which describes the expected total number of seeds produced by a plant of size \( x \), can then be written as

\[
f(x) = s(x) p(x) f_s(x),
\]

where \( s(x) \), \( p(x) \), and \( f_s(x) \) are functions describing the probabilities of survival, flowering, and the expected number of seeds produced by plants of size \( x \), respectively. The survival-growth function is given by

\[
p(y, x) = s(x)[1 - p(x)] g(y, x),
\]

where \( g(y, x) \) is the probability of an individual of size \( x \) growing to size \( y \). Note that because \( g(y, x) \) is a probability density function, individuals of the same size can grow by different amounts, which can be thought of as representing within-year spatial variation in growing conditions. These functions describe the demography of the established plant population. The losses from the seed bank are determined by germination and seed death, which occur with probabilities \( g \) and \( d \), respectively (Rees and Long 1992). Finally, we assume that the probability of seedling establishment is \( p_e \). Putting this together, we obtain a coupled system of equations, namely,

\[
S(t + 1) = (1 - d)(1 - g) S(t) + (1 - g) \int_a^x f(x) n(x, t) dx,
\]

\[
n(y, t + 1) = g(1 - d)p_t f_s(y) S(t) + \int_a^x [p(y, x) + gp, f(y, x)] n(x, t) dx,
\]

where \( S(t) \) is the number of seeds in the seed bank in year \( t \). The seed bank equation is made up of two parts: those seeds that remain in the seed bank and the seeds produced this year, which remain dormant. The established plant population, \( n(y, t + 1) \), is made up of three parts: plants that establish from the seed bank, established plants that survive and grow, and seeds produced this year that germinate and establish. There are several ways of formulating the model, depending on the assumed order of events in the life cycle; however, the simple formulation used here has the desirable property that when \( d = 1 \), there is no establishment from the seed bank.

In both species, the probability of seedling establishment, \( p_e \), is density dependent and given by

\[
P_e = \frac{R}{g[(1 - d)S(t) + \int_a^x f(x) n(x, t) dx]},
\]

where \( R \) is the number of recruits and the denominator is made up of those seeds that germinate from the seed bank and those seeds produced this year that germinate immediately.

This model describes the dynamics of a continuously size-structured plant population with a seed bank in a constant environment; the general properties of this class of models is analyzed in detail by Ellner and Rees (2006a), who present a discussion of the relative advantages of matrix models and IPMs. To extend the model to include temporal variation, we define the functions \( f^{(0)}(x), f^{(1)}(x), x \), and \( p^{(0)}(y, x) \) to be the seed production, fecundity, and survival-growth functions in year \( t \) and let \( R(t + 1) \) be the number of recruits in year \( t + 1 \); the model then becomes

\[
S(t + 1) = (1 - d)(1 - g) S(t) + (1 - g) \int_a^x f^{(0)}(x) n(x, t) dx,
\]

\[
n(y, t + 1) = g(1 - d)p_t f_s^{(0)}(y) S(t) + \int_a^x [p^{(0)}(y, x) + gp, f^{(0)}(y, x)] n(x, t) dx,
\]

where the probability of establishment is given by

\[
P_e(t) = \frac{R(t + 1)}{g[(1 - d)S(t) + \int_a^x f^{(0)}(x) n(x, t) dx]}.
\]

Environments are assumed to be independent and identically distributed. Each year type, \( \tau \), is characterized by the number of recruits in the following year, \( R_{\tau + 1} \), and a pair of functions describing survival and growth, \([s_\tau(x), g_\tau(y, x)]\), which have been estimated from field data. The choice of which aspects of the demography to treat as stochastic depends on the biology of the system and the aims of the study. The approach presented here can readily be extended to include stochasticity in any demographic process. Methods for numerically solving the model are described in appendix B.

*Population Biology of Carlina vulgaris and Carduus nutans*

*Carlina* is a monocarpic thistle of base-rich soils (mainly on limestone or calcareous sand) found as a native over
a wide area in western, central, and eastern Europe and introduced to North America and New Zealand. A detailed description of the *Carlina* study is given by Rose et al. (2002), and so we will give a brief description. The study spanned 16 years, and during this time, the fates of more than 1,400 individuals were followed within permanent quadrats on two 50-m transects. Growth and survival were size dependent and fluctuated from year to year. The survival analysis presented by Rose et al. (2002) contained an error (some plants that had flowered were excluded), and so corrected parameter estimates are given in table A1. Recruitment was independent of the previous year’s seed production and also showed yearly fluctuations, with the number of recruits being mainly determined by the grazing regime (P. J. Grubb, personal observation).

The probability of flowering depended on both plant size and age, although the age component was small and so will be ignored (results from size- and age-dependent models were qualitatively similar; results not presented; for a description of age- and size-dependent IPMs, see Childs et al. 2003, 2004). The fitted logistic regression relating the probability of flowering to plant size defines the flowering strategy in *Carlina*. Mean age at flowering is 3.04 (0.34) years (mean and standard error), with individuals starting flowering in their second year and a maximum age at flowering of 8 years.

*Carduus* is a monocarpic thistle native in Europe, Asia Minor, Siberia, and North Africa, and it has been introduced in most other temperate climate regions of the world. The study site was at Kybeyan in New South Wales, Australia, and plants were followed from 1988 to 1996; a detailed demographic analysis will be presented elsewhere. Every 6 weeks during this period, the fate of all plants in 10 permanent quadrats (0.5 m × 0.5 m) within a 20 × 20-m plot was monitored. Size was measured using the mean radius (based on two measurements), and this was converted to rosette area, assuming the plants are circular. The seed bank was estimated twice a year in spring and autumn by washing and sieving 100 random soil cores (10 cm deep × 3.2 cm diameter; see Woodburn and Sheppard 1996; Shea et al. 2005).

In all analyses, plant size was transformed using natural logarithms. Generalized linear models of the probability of mortality and flowering in *Carduus* were constructed, assuming binomial errors and a logit link function (McCullagh and Nelder 1989). There were large effects of size and year on the probability of survival (size: $\chi^2 = 247.8$, df = 1, $P < .0001$; year: $\chi^2 = 231.4$, df = 6, $P < .0001$; fig. 1a; for parameter estimates, see table A2). Plant size was the most important predictor of flowering ($\chi^2 = 84.8$, df = 1, $P < .0001$), with larger plants being more likely to flower than smaller ones (fig. 1b; parameter estimates and standard errors, intercept: $\beta_0 = -4.99$ (1.07); slope: $\beta_1 = 1.57$ (0.29); this relationship defines the flowering strategy in *Carduus*. Plant size for the next year was independent of current size ($F = 0.3$, df = 1,26, $P > .05$), although there were significant year effects ($F = 4.3$, df = 6,26, $P < .005$). The lack of a significant linear relationship between size this year and next, as found in many other monocarpic species (Metcalfe et al. 2003), is probably a result of most plants either dying or flowering in their first year, resulting in a relatively small sample size ($n = 37$). The number of recruits fluctuated dramatically during the study (range = 2.8–417 m$^{-2}$; fig. 1c), largely driven by climate (average recruit size = 1.79, variance = 1.74, log scale). Seed production was described by a simple allometric relationship, namely, log(seeds) = A + B log(size), with $A = 3.28$ (0.43), $B = 0.58$ (0.07), $r^2 = 0.36$, and $n = 114$. The mean age at flowering is 0.15 (0.04) years, indicating that most individuals behave as annuals, with only 15% of individuals flowering in their second year. There was no relationship between the density of seeds in the seed bank and the subsequent number of recruits ($r = -0.19$, $P > .7$, $n = 8$; fig. 1c, 1d), suggesting that as in *Carlina*, the population was not seed limited (Turnbull et al. 2000).

### Data on Seed Persistence and Dispersal in *Carlina* and *Carduus*

Data on seed banks and germination are notoriously variable (Thompson et al. 1997); however, the seed banks of *Carlina* and *Carduus* have been extensively studied. The two species have very different seed bank characteristics, with *Carlina* forming little or no long-term seed bank (Verkaar and Schenkeveld 1984; Viragh and Gerencser 1988; Levassor et al. 1990; Poschlod and Jackel 1993; Eriksson and Eriksson 1997; de Jong et al. 2000) and *Carduus* often forming large, persistent seed banks with seed bank longevity in the range of 3 to 20+ years (Roberts and Chancellor 1979; Burnside et al. 1981; Popay and Medd 1990; Sindel 1991; Faccini et al. 1992; Wardle et al. 1992; James et al. 1998).

In both species, seeds are wind dispersed, but because the pappus is easily detached, dispersal is limited to within a few tens of meters of the parent plant, although some small proportion of seed will be dispersed over much longer distances (*Carlina*: Greig-Smith and Sagar 1981; Klinkhamer et al. 1996; Løjgren et al. 2000; Franzen and Eriksson 2003; *Carduus*: Lee 1977; Smith and Kok 1984; Kelly et al. 1988). In *Carduus*, gene flow via pollen dispersal has also been quantified, and this appears to occur over shorter distances than seed dispersal (Smyth and Hamrick 1987). These results suggest that seed dispersal and pollen dispersal in *Carduus* occur on approximately the same spatial scale as the populations studied.
Patterns of Temporal Variation in Demographic Rates

To compare the patterns of temporal variation in survival, we calculated the variance in survival probability for a given plant size using the yearly parameter estimates (tables A1, A2). This was then averaged with respect to size, assuming all sizes between the minimum and maximum were equally likely. The same procedure was used for temporal variation in growth. Variation in recruitment was quantified using the coefficient of variation, $CV = \sigma/\mu$.

Invasibility Analysis and the ESS

Flowering/Germination Strategy

In a variable environment, fitness is determined by the invasion exponent, $\theta$, defined by

$$\theta = \lim_{t \to \infty} t^{-1}E[\ln(N_t)],$$

where $N_t$ is the total population size at time $t$ (Metz et al. 1992). The number $\theta$ is equal to the stochastic growth rate of an invading mutant population in the environment.
set by the resident; that is, \( \theta = \log \lambda_\circ \) and so if \( \theta \) is negative, the invader will become extinct. We assume that the invader and the resident experience the same sequence of environments and differ only in their germination and flowering strategies. To estimate \( \theta \), we assume that the invader is rare, and so its density has no effect on the population growth rate. We then generate a time series (5,000 years) for the resident population, consisting of the year type \( (\tau_1, \tau_2, \ldots, \tau_{5,000}) \) and the probability of establishment \( [p^R_1(1), p^R_2(2), \ldots, p^R(5,000)] \). This defines the environment in which we estimate \( \lambda_\circ \). We calculate \( \theta \) by iterating the model for the invader, using the resident time series for \( \tau \) and replacing \( p_\tau(t) \) in equation (6) with \( p^R_\tau(t) \). The maximum likelihood estimator of the invader growth rate, \( \hat{\theta} \), is then given by

\[
\hat{\theta} = \frac{\ln (N_t) - \ln (N_{t-1})}{t-1},
\]

where \( N_t \) is the total population size at time \( t \). Ellner and Rees (2006b) prove that for a wide class of stochastic IPMs, including those considered here, the stochastic growth rate \( (8) \) exists and may be computed using equation (9). We use equation (9) to generate a fitness landscape describing the growth rate of mutant strategies invading a resident population. Landscapes were generated by estimating \( \lambda_\circ \) (= \( e^\theta \)) on a fixed grid of parameter values. To calculate the ESS, we used an iterative invasion algorithm (app. B).

To obtain an estimate of the range of strategies that are biologically consistent with the ESS estimates, we calculated the set of strategies that have fitness \( \exp(\theta) > 0.99 \), assuming the resident uses the ESS strategy. These strategies have at most a 1% fitness difference compared with the ESS. It is important to do this because when fitness landscapes are relatively flat, very different strategies may have similar fitnesses.

These models assume that the within-study site dynamics correctly capture the spatial and temporal variations in fitness that genotypes experience. However, because temporal variation may occur on scales smaller or larger than the study populations, we extended the models to include spatial population structure (app. C). These models show that the qualitative predictions of the models are robust to the inclusion of spatial structure.

**Alternative Models for Demography**

In order to understand how the ESS flowering strategy and germination probability are influenced by different sources of temporal variation, nonlinear averaging, and nonequilibrium dynamics, we derive appropriately averaged survival and growth functions (for details of the calculations, see app. B; for background information, see Rees et al. 2004). Comparison of the ESS predictions from the different models then allows the impact of stochastic effects to be estimated. A single alternative model for recruitment was derived by replacing \( R \) with the mean number of recruits. We refer to this as the average recruitment model. This excludes the effects of nonequilibrium dynamics induced by stochastic recruitment. To partition the effects of nonlinear averaging and nonequilibrium dynamics in growth and survival, we constructed three alternative models, giving rise to four models in each case. In the first, referred to as the average environment (AE) model, we replace the yearly intercepts with their mean value. This AE model eliminates the effects of both nonlinear averaging and nonequilibrium dynamics. In the second model, referred to as the nonlinear averaging (NLA) model, we average the growth and survival functions with respect to the distribution of intercepts. The resultant model captures the effects of nonlinear averaging without including nonequilibrium dynamics. The third model, referred to as the nonequilibrium dynamics (NED) model, captures the effects of nonequilibrium dynamics by subtracting the effect of nonlinear averaging from the yearly models of survival and growth. The model using the average recruitment and the average-environment growth and survival functions is referred to as the constant environment model.

**Partitioning the Effects of Temporal Variation**

To partition the effects of temporal variation in the vital rates on the ESS flowering/germination strategy, we used an ANOVA decomposition of the different stochastic effects. By comparing the predictions of models using the AE and NLA survival and/or growth functions, we can estimate the effect of nonlinear averaging. Comparing the predictions of models incorporating the AE survival and/or growth functions with those using the NED models allows the effect of nonequilibrium dynamics to be estimated. Interactions between the effects of nonlinear averaging and nonequilibrium dynamics can then be estimated by comparing the predictions of the original stochastic model against the estimates of the main effects. We write the mean ESS strategy in the fully stochastic environment, \( \mu_v \), as a linear function of the corresponding mean for a constant environment, \( \mu_c \), a stochastic recruitment effect, \( \Delta R_v \), stochastic survival effects, \( \Delta S_{NLA} \) and \( \Delta S_{NED} \), stochastic growth effects, \( \Delta G_{NLA} \) and \( \Delta G_{NED} \), and first-order interaction terms, such that

\[
\mu_v = \mu_c + \Delta R_v + \Delta S_{NLA} + \Delta S_{NED} + \Delta G_{NLA} + \Delta G_{NED} + \text{interactions},
\]
where the NLA and NED subscripts refer to the effect of nonlinear averaging and nonequilibrium dynamics, respectively. To estimate these effects, the ESS flowering/germination strategy was calculated using every combination of AE, NLA, NED, and stochastic models for survival, growth, and recruitment. The resultant design of the simulation experiment is a five-way fully factorial ANOVA. The size slope of the flowering function, $\beta_s$, was constrained at the estimated value during the simulation experiment to prevent the flowering surface from becoming a step function. There are several reasons why it might be impossible for plants to achieve a step function: there is variable growth between the decision to flower being made and when plant size is measured, plant size may not be perfectly correlated with the threshold condition for flowering, and there may be genetic variation in the threshold condition for flowering. Results for models where the size slope of the flowering function, $\beta_s$, was not constrained are presented by Rose et al. (2002) and Childs et al. (2003, 2004). We explored models, including all main effects and first-order interactions; this was then simplified using a stepwise procedure so that only significant terms remained in the model. Nonsignificant main effects were retained if interactions containing them were significant.

The ANOVA models were fitted to the ESS average size at flowering, calculated using the methods described by Childs et al. (2004). Analyses of the ESS germination probability were performed on a logistic scale, so the fitted values lie in the unit interval. To explore the consequences of covariation between yearly parameter estimates, we randomized the order of the yearly coefficients and repeated the analysis described above 50 times. For each randomized parameter set, the ANOVA model, equation (10), was fitted, and the Spearman rank correlation, $r_s$, between the yearly parameter estimates was calculated.

### Results

**Demographic Variation**

In both species, there are temporal fluctuations in growth, survival, and recruitment (table 1); however, these are more extreme in *Carduus*. These fluctuations in demographic rates generate variation in fitness from year to year, and so the necessary condition for the evolution of seed dormancy, as a result of bet hedging, is satisfied in both species. In *Carlina*, there is no evidence of covariation between the yearly parameter estimates (Rose et al. 2002); however, in *Carduus*, there is evidence of a positive correlation between the survival intercepts and the number of recruits the following year (fig. 2).

### Table 1: Comparison of the patterns of temporal variation in growth, $\sigma^2_g$, survival, $\sigma^2_s$, and recruitment in *Carlina* and *Carduus*

<table>
<thead>
<tr>
<th>Species</th>
<th>$\sigma^2_g$</th>
<th>$\sigma^2_s$</th>
<th>$CV$ recruitment</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Carlina</em></td>
<td>0.04</td>
<td>1.37</td>
<td>0.81</td>
</tr>
<tr>
<td><em>Carduus</em></td>
<td>1.28</td>
<td>6.48</td>
<td>1.21</td>
</tr>
</tbody>
</table>

**Evolution of Size-Dependent Flowering and Seed Dormancy**

In both species, it is difficult to obtain reliable estimates of seed mortality, and so we explored the model predictions for a wide range of seed death rates, $d \in [0.01, 0.99]$. We allowed both the probability of germination and the intercept of the flowering function, $\beta_o$, to evolve simultaneously. For *Carlina*, we find that complete germination is the ESS germination strategy for all seed death rates (fig. 3a) and that the ESS $\beta_o \approx -12$ is in excellent agreement with the data (fig. 3b). For the ESS $\beta_o$, the 99% fitness sets are relatively small, indicating that the ESSs are well characterized; in contrast, for the ESS germination probability, the 99% fitness sets become larger as the seed mortality decreases. This occurs because in a constant environment, the only cost of delayed germination is through seed mortality, and so when there is very little seed mortality, germination becomes an approximately neutral character.

In *Carduus*, the ESS germination probability is $<1$ for all seed death rates $d \approx 0.95$ (fig. 3c), and as expected for high rates of seed mortality, the ESS germination fraction is 1. There is excellent agreement between the ESS $\beta_o$ and the estimated value, with the ESSs lying within the 95% confidence interval for all seed death rates (fig. 3d). For both characters, the 99% fitness sets are relatively small, suggesting that the ESSs are well characterized.

To test whether the predicted strategies are in fact ESSs, we computed the fitness landscape for the joint flowering and germination strategy, assuming that the probability of seed mortality was 0.2 (fig. 4; other values give similar results, not presented). For both species, the putative ESSs correspond to fitness maxima, indicating that these strategies are invadable by other strategies.

To test whether the lack of seed dormancy in *Carlina* was a consequence of the adults being relatively long lived or there being smaller demographic fluctuations from year to year, we calculated the ESS germination probability assuming the probability of flowering was 1 for all plant sizes, and so *Carlina* behaves as an annual. For all seed death rates $d \in [0.01, 0.99]$, the ESS was complete germination, suggesting that the lack of seed dormancy was a consequence of the relatively small demographic fluctuations from year to year (table 1).
Figure 2: Patterns of covariance between the Carduus parameter estimates. a, Yearly survival and growth intercepts ($r_t = 0.29, P > .50$). b, Survival intercepts and the number of recruits the following year ($r = 0.79, P < .06$). c, Growth intercepts and the number of recruits the following year ($r = 0.07, P > .5$). d, Survival intercepts in year $t$ and growth intercepts in year $t + 1$ ($r = -0.66, P < .2$).

**Partitioning the Effects of Temporal Variation**

The ANOVA model partitioning of the effects of stochastic selection pressures on the joint ESS flowering and germination strategies is presented in table 2. Complete germination is the ESS strategy in both constant and variable environments for Carlina, so there are no significant stochastic selection pressures. In contrast, in Carduus, the nonequilibrium demographic fluctuations induced by variation in recruitment and survival ($\Delta R_v$ and $\Delta S_{ned}$) are highly significant and negative, demonstrating how temporal variation can select for the evolution of seed dormancy. The interaction between these terms ($\Delta R_v \times \Delta S_{ned}$) is also significant and positive and of roughly the same magnitude as the main effects, suggesting that variation in recruitment and survival are partly substitutable.

For flowering in Carlina, none of the interactions was significant, and the main effects accounted for 91% of the variation in ESS flowering size. In contrast, in Carduus, the interaction terms accounted for 41% of the variation and so were retained in the model. In both species, variable recruitment selects for larger sizes at flowering, which sug-
Waiting Games

Figure 3: Effect of varying seed mortality, $d$, on the Carlina joint evolutionarily stable strategy germination probability ($a$) and flowering intercept ($b$); the horizontal line is the estimated parameter value ($-11.78$), and the shaded box is the 95% confidence interval (CI). $c$, $d$, Equivalent graphs for Carduus. The horizontal line in $d$ is the estimated parameter ($-4.99$), and the shaded box is the 95% CI. The vertical lines through the points define the set of strategies with fitness greater than 0.99.

suggests the operation of a bet hedging strategy. Nonequilibrium dynamics generated by fluctuations in survival, $\Delta S_{\text{NED}}$, and growth, $\Delta G_{\text{NED}}$, select for smaller sizes at flowering in Carlina because this reduces the chance that individuals will experience a low survival/growth year. In both species, nonlinear averaging of the growth function, $\Delta G_{\text{NLA}}$, selects for larger sizes at flowering, and in Carlina, nonlinear averaging of the survival function, $\Delta S_{\text{NLA}}$, selects for smaller sizes at flowering. In Carduus, the $\Delta G_{\text{NLA}} \times \Delta G_{\text{NED}}$ interaction is negative, indicating that the positive effect of $\Delta G_{\text{NLA}}$ is reduced in the presence of nonequilibrium growth dynamics.

In Carduus, there are highly significant interactions between $\Delta R_{\text{S}}$ and $\Delta S_{\text{NED}}$ and between $\Delta S_{\text{NED}}$ and $\Delta G_{\text{NED}}$ for the flowering strategy (table 2). We conjecture that these interactions are a consequence of the covariation between the yearly parameter estimates (fig. 2). This idea is supported by the results from the simulation experiments where we randomized the yearly survival intercepts. In both cases, we find strong correlations between the co-
Figure 4: Fitness landscapes for Carlina (a) and Carduus (b), assuming that the resident is at the joint germination probability, g, and flowering intercept, β₀ (evolutionarily stable strategy). The resident strategy is marked with a dot; in both cases, the probability of seed death, d, was set at 0.2.

Discussion

The predictions of the evolutionary models are in remarkable agreement with the field data. We can predict not only the ESS flowering strategy, β₀, in the field for both species but also the lack of seed dormancy in Carlina and substantial seed dormancy in Carduus. The partitioning of stochastic selection on size at flowering reveals a substantial impact of stochastic selection in Carlina even though the net effect is small (65 mm average size at flowering in constant environment vs. 61 mm in fully stochastic case; table 2). Summing the absolute values of the stochastic effects suggests that stochastic terms are equal to \( \approx 40\% \) of the stochastic environment ESS; similar results are given by Rees et al. (2004) for a more complex model where the probability of flowering is both size and age dependent. In Carduus, where there are more substantial demographic fluctuations (table 1), the net effect of stochastic selection is considerable (64 cm² average size at flowering in constant environment vs. 139 cm² in fully stochastic case; table 2). The sum of the absolute values of the stochastic effects is \( \approx 310 \) cm², which is roughly two times the stochastic environment ESS value.

Variation in recruitment selects for larger sizes at flowering in both species, which indicates that a bet hedging mechanism is operating. To spread the risk of suffering a poor year for recruitment, a particular flowering strategy needs to distribute reproduction over several years. When individuals are subject to variable growth (within or between years), increasing the size at flowering achieves this by increasing the variance in the age at flowering. In contrast, the nonequilibrium dynamics induced by variable survival and growth in Carlina select for smaller flowering sizes. Presumably, this reflects the cost associated with occasional low-survival or low-growth years; individuals that wait too long before flowering increase the risk of suffering such an event.

Table 2: Estimated effects of the different sources of stochastic variation on the evolutionarily stable flowering/germination strategy in Carlina and Carduus

<table>
<thead>
<tr>
<th>Term</th>
<th>Carlina</th>
<th>Carduus</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \mu_c )</td>
<td>64.95***</td>
<td>63.62***</td>
</tr>
<tr>
<td>( \Delta R_n )</td>
<td>4.22***</td>
<td>40.40***</td>
</tr>
<tr>
<td>( \Delta S_{NLA} )</td>
<td>-5.52***</td>
<td>2.61</td>
</tr>
<tr>
<td>( \Delta S_{NED} )</td>
<td>-1.60*</td>
<td>12.74</td>
</tr>
<tr>
<td>( \Delta G_{NLA} )</td>
<td>5.76***</td>
<td>86.24***</td>
</tr>
<tr>
<td>( \Delta G_{NED} )</td>
<td>-6.94***</td>
<td>23.87</td>
</tr>
<tr>
<td>( \Delta R_n \times \Delta S_{NED} )</td>
<td>-90.94***</td>
<td>7.20***</td>
</tr>
<tr>
<td>( \Delta S_{NED} \times \Delta G_{NED} )</td>
<td>51.45**</td>
<td></td>
</tr>
<tr>
<td>( \Delta G_{NLA} \times \Delta G_{NED} )</td>
<td>-50.23***</td>
<td></td>
</tr>
<tr>
<td>( r^2 )</td>
<td>.91</td>
<td>.94</td>
</tr>
</tbody>
</table>

Note: The probability of seed death, d, was set at 0.2; \( \mu_c \) is the mean flowering size in Carlina (mm) and in Carduus (cm²).

* \( P < .05 \)

** \( P < .01 \)

*** \( P < .001 \)
Figure 5: Relationships between the covariance of the yearly parameter estimates and effect size of the $\Delta R_v \times \Delta S_{NED}$ and $\Delta S_{NED} \times \Delta G_{NED}$ interactions for the Carduus joint evolutionarily stable flowering strategy. All relationships are significant at $P < .0001$; $r_s(m_i + \gamma, R_{1,i})$ is the Spearman rank correlation between the yearly survival intercepts and the number of recruits the following year, and $r_s(m_i + \gamma, a_i + \alpha)$ is the Spearman rank correlation between the yearly survival and growth intercepts.

The results from the simulation experiment, where we randomized the order of the yearly survival intercepts, clearly indicate the importance of covariation between different forms of stochasticity. Positive covariance between survival and recruitment or survival and growth makes the environment effectively more variable as good years are very good and vice versa. In contrast, negative covariation has the opposite effects because years that are bad for, say, survival are good for growth or recruitment. Whether covariance selects for larger or smaller sizes at flowering then depends on which aspects of the demography are variable (cf. fig. 5a, 5b, where the relationships are negative and positive, respectively). The $\Delta R_v \times \Delta S_{NED}$ and $\Delta S_{NED} \times \Delta G_{NED}$ interactions, which have significant effects on the ESS size at flowering in Carduus, appear to be a result of covariation between the yearly parameter estimates (fig. 5). Survival and subsequent recruitment are positively correlated (fig. 2b), which means there are few recruits after a low-survival year and vice versa. Apparently, the former effect outweighs the latter, leading to selection for smaller sizes at flowering. In contrast, when survival and subsequent recruitment are negatively correlated, we see the opposite effect (fig. 5a). The $\Delta S_{NED} \times \Delta G_{NED}$ interaction is related to the strength of covariation between growth and survival. When good years for growth are also good years for survival, the $\Delta S_{NED} \times \Delta G_{NED}$ interaction is positive, leading to selection for larger sizes at flowering.

The partitioning of stochastic selection pressures on the germination probability in Carlina is particularly simple because complete germination is the ESS in both constant and stochastic environments, and so none of the fitted terms is significant (table 2); see Ellner’s (1985) discussion of when complete germination is an ESS in a stochastic environment. In contrast, in Carduus, the $\Delta R_v$ and $\Delta S_{NED}$ terms are negative and highly significant, demonstrating that nonequilibrium fluctuations in demography are important in selecting for seed dormancy. The interaction between these terms indicates that these effects are roughly substitutable (ESS germination with either recruitment or survival variation is $\approx 0.45$, with both $\approx 0.30$). This argues for the need to test quantitatively theoretical predictions because in both species, there is temporal variation in recruitment, growth, and survival, yet only in Carduus is this sufficient to select for seed dormancy. There is no evidence that species with greater seed dormancy can have riskier flowering strategies; as in Carduus, the ESS flowering strategy is independent of the ESS germination probability (fig. 3d).

The prediction that Carlina, which has relatively long-lived adults and high variance in the age at flowering, should have less seed dormancy than Carduus is consistent with the models presented by Rees (1993, 1994). In these
models, adult longevity was fixed, and seed dormancy was allowed to evolve in response to temporal variation in the environment. Species with long-lived adults produce seeds in many years and so reduce the effect of temporal variation, and this selects for less seed dormancy. In monocarpic perennials, such as *Carlina*, age at flowering is highly variable, which reduces the impact of environmental variation and so selects for less seed dormancy. However, in *Carlina*, the lack of seed dormancy is not a consequence of flowering being spread across years but a result of the relatively small demographic fluctuations, as demonstrated by the simulation studies where *Carlina* was made to behave as an annual. This clearly indicates the need to test theoretical predictions quantitatively because qualitative tests can be misleading. This is likely to be a common problem because in stable environments, selection favors delayed reproduction and less dormancy, whereas in more variable environments, selection favors early reproduction and dormant seeds (Bulmer 1984, 1985). This naturally leads to a negative correlation between adult longevity and seed dormancy, as found in several comparative studies (e.g., Rees 1993, 1996). Whether this pattern is the result of long-lived adults buffering the population from demographic fluctuations or systematic variation in magnitude of demographic fluctuation clearly cannot be determined by comparative analyses of trait values alone.

The work illustrates that a detailed understanding of why established plants delay reproduction or have dormant seeds can be obtained by parameterizing population models using long-term field data. The models emphasize that it is important to quantify not only the variance in demographic rates but also their covariance. The importance of covariation between demographic rates has recently been emphasized by Doak et al. (2005), who show that the classical result, that temporal variation in demographic rates negatively influences fitness and population growth, is a consequence of ignoring the correlation between demographic rates. Their analysis shows that positive correlations enhance stochastic sensitivities, whereas negative correlations have the opposite effect and can even result in variability increasing fitness or population growth (Doak et al. 2005).

Acknowledgments

For comments on the manuscript at various stages, we thank S. Ellner, R. Freckleton, and an anonymous reviewer whose comments were especially helpful. We should particularly like to thank K. Shea and T. Woodburn for help organizing the *Carduus* data set and useful discussions during the early stages of the project. Research support was provided by Natural Environment Research Council grant NER/A/S/2002/00940 (M.R.).

APPENDIX A

Parameter Estimates for the Growth and Survival Models

In this appendix, we give details of the fitted models for *Carlina* and *Carduus*. For survival, we fit generalized linear models relating the probability of survival to log plant size; for growth in *Carduus*, we model size in year \( t + 1 \) as

\[
L(t + 1) = a_s + \alpha_s + \epsilon,
\]

where \( a_s + \alpha_s \) is the intercept in year \( t \) and \( \epsilon \) describes the within-year scatter. In *Carlina*, the fitted growth models are given by Rose et al. (2002); note, however, that unlike in *Carduus*, the growth equation is

\[
L(t + 1) = a_g + \alpha_g + b_g L(t) + \epsilon.
\]

Table A1: Summary of the statistical analysis for survival in *Carlina*

<table>
<thead>
<tr>
<th>Year</th>
<th>( m_0 + \gamma_s )</th>
<th>( m_s )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1979–1980</td>
<td>-3.28 (.64)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1980–1981</td>
<td>-1.68 (.53)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1981–1982</td>
<td>-4.25 (.61)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1982–1983</td>
<td>-2.07 (.60)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1983–1984</td>
<td>-2.77 (.87)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1984–1985</td>
<td>-2.22 (.85)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1985–1986</td>
<td>-1.58 (.50)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1986–1987</td>
<td>-1.83 (.50)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1987–1988</td>
<td>-2.56 (.46)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1988–1989</td>
<td>-3.19 (.61)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1989–1990</td>
<td>-1.67 (.45)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1990–1991</td>
<td>-0.93 (.50)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1991–1992</td>
<td>-1.94 (.47)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1992–1993</td>
<td>-2.75 (.45)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1993–1994</td>
<td>-4.07 (.50)</td>
<td>.90 (.13)</td>
</tr>
<tr>
<td>1994–1995</td>
<td>-3.50 (.82)</td>
<td>.90 (.13)</td>
</tr>
</tbody>
</table>

Note: The values in each column are the parameter estimates, with standard errors in parentheses; \( m_0 + \gamma_s \) and \( m_s \) are the intercepts and size-dependent slope of the fitted logistic survival regressions, respectively.

Table A2: Summary of the statistical analyses for growth and survival in *Carduus*

<table>
<thead>
<tr>
<th>Year</th>
<th>( a_s + \alpha_s )</th>
<th>( m_0 + \gamma_s )</th>
<th>( m_s )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988–1989</td>
<td>4.28 (.27)</td>
<td>-4.71 (.30)</td>
<td>1.03 (.09)</td>
</tr>
<tr>
<td>1989–1990</td>
<td>5.30 (.99)</td>
<td>-5.60 (.50)</td>
<td>1.03 (.09)</td>
</tr>
<tr>
<td>1990–1991</td>
<td>5.86 (.44)</td>
<td>-2.44 (.92)</td>
<td>1.03 (.09)</td>
</tr>
<tr>
<td>1991–1992</td>
<td>3.32 (.30)</td>
<td>-4.11 (.35)</td>
<td>1.03 (.09)</td>
</tr>
<tr>
<td>1992–1993</td>
<td>3.58 (.99)</td>
<td>-7.12 (1.05)</td>
<td>1.03 (.09)</td>
</tr>
<tr>
<td>1993–1994</td>
<td>3.40 (.44)</td>
<td>-2.32 (.57)</td>
<td>1.03 (.09)</td>
</tr>
<tr>
<td>1994–1995</td>
<td>2.77 (.99)</td>
<td>-9.42 (1.01)</td>
<td>1.03 (.09)</td>
</tr>
</tbody>
</table>

Note: \( \sigma^2 = 0.97 \). The values in each column are the parameter estimates, with standard errors in parentheses; \( a_s + \alpha_s \) is the growth intercept in year \( t \), the slope was not significantly different from zero, \( \sigma^2 \) is the residual variance from the fitted regression, and \( m_0 + \gamma_s \) and \( m_s \) are the intercepts and size-dependent slope of the fitted logistic survival regressions, respectively.
APPENDIX B
Numerical Methods and Alternative Demographic Models

In this appendix, we give some details of the numerical calculations used in the main text. Specifically, we describe the implementation of the models on a computer and the calculation of the evolutionarily stable strategies (ESSs), and we give the equations to calculate the various survival and growth functions used to partition the effects of temporal variation on the joint ESS.

Numerical Solution of the Integral Projection Model

To solve the model, we use numerical integration methods (Easterling et al. 2000). Specifically, we use the midpoint rule, which is the most straightforward to implement. If each component function is evaluated at \( q \) equally spaced quadrature mesh points, \( y_i \), and \( w \) is the quadrature weight (difference between the \( y_i \)'s), we can then approximate equation (4) in the main text as

\[
\begin{align*}
K &= \begin{bmatrix}
(1 - d)(1 - g) & (1 - g)f(y_i)w & \cdots & (1 - g)f(y_i)w \\
\frac{g(1 - d)p_f(y_i)}{1} & \left[ p(y_0, y_i) + gp_f(y_0, y_i) \right]w & \cdots & \left[ p(y_0, y_i) + gp_f(y_0, y_i) \right]w \\
\vdots & \vdots & \ddots & \vdots \\
\frac{g(1 - d)p_f(y_i)}{1} & \left[ p(y_r, y_i) + gp_f(y_r, y_i) \right]w & \cdots & \left[ p(y_r, y_i) + gp_f(y_r, y_i) \right]w
\end{bmatrix} .
\end{align*}
\]  

(B2)

The resulting model can then be analyzed using standard matrix software. When implementing the model on a computer, it is important to decide whether the \( n(y, t) \) stores values of the density function, and so in order to calculate total population size has to be integrated, or the integrated density function \( \tilde{n}(y, t) \), in which case it can just be summed.

For the stochastic model, define \( K^{(t)} \) as the matrix (eq. \( [B2] \)) in year \( t \), calculated using the appropriate growth, survival, and recruitment for that year. We can then iterate the stochastic integral projection model numerically by matrix multiplication,

\[
n(t + 1) = K^{(t)}K^{(t-1)} \cdots K^{(0)}n(0).
\]

For all the models described in the main text, we used 50 quadrature mesh points. Increasing this had no meaningful effect on the model solutions.

Calculation of the ESS

To determine the ESS, we used an iterative invasion procedure. We started the invasion process using an initial parameter vector to generate a resident time series and then maximized the invasion exponent (\( \theta_{\text{max}} \)) for a rare invader with different germination and flowering strategy using the Nelder-Mead algorithm (Nelder and Mead 1965), giving a new set of parameters (\( \Theta_{\text{max}} \)). These parameters were then used to generate a new resident time series and a second search performed to determine the new \( \Theta_{\text{max}} \). This process was repeated until successive values of \( \theta_{\text{max}} \) converged on 0 to a specified tolerance (0.001). The last \( \Theta_{\text{max}} \) was taken to be the putative ESS. The germination probability, \( g \), must lie in the unit interval, and so when performing the maximization, we used a logistic scale, \( g = \exp(q)/(1 + \exp(q)) \). This means that complete germination is not possible; however, to simplify presentation, we will say that complete germination was the ESS whenever the predicted ESS germination probability was greater than 0.999.
Alternative Models of Demography

We now describe the calculation of the average environment (AE), nonlinear average (NLA), and nonequilibrium dynamics (NED) growth and survival models (for further details, see Rees et al. 2004). The NLA survival function was evaluated numerically using

\[ N \left( \frac{1}{Z} \exp \left( \frac{m}{H^{1001}} \frac{g}{H^{1001}} \right) x \right) = \frac{1}{1 + \exp \left( \frac{m}{H^{1001}} \frac{g}{H^{1001}} \right) N} \]  

where \( m_0 \) and \( m_s \) are the average intercept and the size-dependent slope, respectively; \( g_t \) is the yearly deviation from the average intercept; and the \( s \) subscript indicates that this model contains components that are due to temporal variation (i.e., nonzero \( g_t \) terms). The average environment survival model is

\[ s(x) = \exp \left( \frac{m}{H^{1001}} \frac{g}{H^{1001}} mx \right). \]  

The functions \( \tilde{s}_x(x) \) and \( \tilde{s}(x) \) are referred to as the NLA and AE survival functions, respectively. The NED survival function, \( \tilde{s}_x(x) \), was generated using

\[ \tilde{s}_x(x) = s_x(x) - (\tilde{s}_x(x) - \tilde{s}(x)), \]  

where \( s_x(x) \) is the fitted survival function in year type \( x \). The expectation of equation (B5), with respect to the distribution of yearly intercepts, is \( \tilde{s}(x) \). The bracketed term on the right of equation (B5) represents the change in the survival probability due to nonlinear averaging of the survival function. Therefore, the effect of nonequilibrium dynamics can be isolated by subtracting this from the year-specific survival function. To ensure that \( \tilde{s}_x(x) \in [0, 1] \), the function was truncated to lie inside the unit interval. The expectation of the truncated functions was compared against \( \tilde{s}(x) \) and found to give the same ESS predictions.

The NLA growth function is derived in an analogous manner, with \( \tilde{g}_x(y, x) \) being the average of the year-specific growth functions such that

\[ \tilde{g}_x(y, x) = \frac{1}{N} \sum_{i=1}^{N} \left( a_i + \alpha_x + b_i x \right), \]  

where \( a_i \) and \( b_i \) are the average intercept and the size dependent slope, respectively; \( \sigma^2 \) is the variance about the growth line; and \( \alpha_x \) is the yearly deviation from the average intercept. The \( s \) subscript again indicates that this model contains components that are due to temporal variation (i.e., nonzero \( \alpha_x \) terms). The average environment growth model is

\[ \tilde{g}(y, x) = \frac{1}{\sigma(2\pi)^{1/2}} \exp \left( -\frac{(y - (a_x + \alpha_x + b_y x))^2}{2\sigma^2} \right). \]  

The functions \( \tilde{g}_x(y, x) \) and \( \tilde{g}(y, x) \) are referred to as the NLA and AE growth functions, respectively. These are used to generate the NED growth function, \( \tilde{g}_x(y, x) \), as follows:

\[ \tilde{g}_x(y, x) = g_x(y, x) - [\tilde{g}_x(y, x) - \tilde{g}(y, x)], \]  

where \( g_x(y, x) \) is the fitted growth function in year type \( x \). The expectation of equation (B8), with respect to the distribution of yearly intercepts, is \( \tilde{g}(y, x) \). To ensure that \( \tilde{g}_x(y, x) \in [0, 1] \), the function was truncated to lie inside the unit interval and then renormalized so that the conditional growth function is a true probability density function. The expectation of the truncated functions was compared against \( \tilde{g}(y, x) \) and found to give the same ESS predictions.
APPENDIX C

Spatial Models

In applying the models discussed in the main text of the article, we have ignored complications arising from spatial structure, assuming that the populations were studied at the appropriate spatial scale. In reality, all populations have spatial structure, and this can influence the predictions of models in at least two distinct ways. First, temporal variation in demography may occur at scales larger than the study population, but the study population may form part of a larger spatially extended population linked by dispersal, and within a year, a different subpopulation may experience different environments. In this case, the fitted demographic models, described in the main text, accurately describe the patterns of spatial and temporal variation in demography that individuals within subpopulations experience. However, these models do not accurately describe the patterns of spatial and temporal variation in demography.

![Figure C1](image)

**Figure C1**: Effect of varying the probability of seed dispersal, $D$, on the *Carlina* joint evolutionarily stable strategy germination probability ($a$) and flowering intercept ($b$); the horizontal line is the estimated parameter value ($-11.78$), and the shaded box is the 95% confidence interval. $c$, $d$, Equivalent graphs for *Carduus*. The horizontal line in $d$ is the estimated parameter ($-4.99$), and the shaded box is the 95% confidence interval. The symbols indicate the number of patches in the system and are consistent across all panels. In all cases, we assumed that the probability of seed death was 0.2.
demography that genotypes experience because genotypes are dispersed across subpopulations and so within a year may experience several different environments. In this case, our estimates of the temporal variation that genotypes experience will be overestimated, whereas the estimates of spatial variation will be underestimated. In the second case, temporal variation may occur at scales smaller than the study population, which has the opposite effect, leading to an underestimation of temporal variability as a result of averaging over subpopulations when fitting the demographic models and overestimations of spatial variability.

To extend the models described in the main text to include space, we assumed that the population occurs in \( n \) patches with independent environments and that a fraction \( D \) of the new seeds produced by a given patch disperse at random among all the patches; the remaining fraction \((1 - D)\) stays put, and old seeds in the seed bank and adults also stay put. For the first scenario, where
temporal variation occurs on larger spatial scales than the study population, we explored the sensitivity of the model predictions by estimating the joint ESS germination and flowering strategy for multipatch systems ($n \in \{1, 2, 4, 8, 16, 32\}$) with varying levels of seed dispersal ($D \in \{0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0\}$). We explored the complete range of dispersal probabilities in the simulation experiment although realistically we would expect only a very small fraction of seeds to disperse sufficiently far that they experience an environment that is independent of the patch in which they were produced. The results show that the joint ESS flowering strategy for single-patch and multipatch systems is similar for all levels of seed dispersal (fig. C1b, C1d). For Carlina, complete germination is also the ESS for all multipatch systems (fig. C1a). However, in Carduus, increasing the number of patches or fraction of seeds dispersing results in a systematic increase in the ESS germination probability (fig. C1c). This occurs as a result of selection for delayed germination being driven by fluctuations in the environment that disappear when seeds disperse over a number of independent patches (Bulmer 1984). However, given realistic patterns of seed and pollen dispersal, it seems extremely unlikely that more than a very small proportion ($\leq 1\%$) of seeds/pollen will disperse far enough to experience multiple independent environments. There is a tendency for the ESS flowering intercept to decrease in multipatch systems; this is seen most clearly in Carduus (fig. C1d) with high seed dispersal. This implies that plants adopt a more risky flowering strategy (flower larger) in less variable systems (i.e., those consisting of many well-connected patches), in agreement with the results in the main text. In simulations with no dispersal, the results for single-patch and multipatch systems are identical, and in single-patch systems, the joint ESS is independent of seed dispersal, as expected.

In the second scenario, where temporal variation occurs at scales smaller than the study population, the simulation procedure is more involved because we need to combine data from multiple patches before fitting the statistical models, which mimics what an investigator would do if he or she were unaware of the spatial structure within the study population. The outline of the simulation procedure is as follows: first, calculate the true joint ESS for the multipatch system ($n = 2$ in this case); second, for each year of the simulation, convert the integral projection model into an individual-based stochastic realization for each patch; third, combine the “data” from each patch and refit the statistical models describing growth and survival and calculate the total number of recruits; and finally, using the statistical models estimated in the third step, recalculate the joint ESS assuming the population consists of a single patch.

When refitting the demographic models in the third step, we used nonoverlapping 50-year windows of data. The use of a 50-year window represents a compromise between sampling the different two-patch environments (there are 49 for Carduus and 256 for Carlina) and memory limitations. The use of a two-patch model assumes that within the study population individuals in different patches experience independent environments, which is a fairly extreme deviation from the model assumptions because it is highly likely that within a year plant performance will be correlated across patches. In the simulation experiment, we varied seed dispersal, $D \in \{0, 0.2, 0.4, 0.6, 0.8, 1.0\}$, and seed mortality, $d \in \{0.01, 0.2, 0.4, 0.6, 0.8, 0.99\}$, in all factorial combinations. The simulations demonstrate that the results presented in the main text of the article are robust to incorrectly specifying the spatial scale of temporal fluctuations (fig. C2). A more detailed analysis of the spatial models will be presented elsewhere (D. Z. Childs, M. Rees, J. C. Metcalf, K. E. Rose, A. W. Sheppard, and P. J. Grubb, unpublished manuscript).

**Literature Cited**


