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Mathias, A. and Kisdi, E.

IIASA Interim Report
June 1999

Mathias, A. and Kisdi, E. (1999) Evolutionary Branching and Coexistence of Germination Strategies. IIASA Interim Report. IIASA, Laxenburg, Austria, IR-99-014 Copyright © 1999 by the author(s). http://pure.iiasa.ac.at/5925/

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Interim Report **IR-99-014**

Evolutionary branching and coexistence of germination strategies

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June 1999

IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 34

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

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A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

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Acknowledgments

We thank Géza Meszéna and Stefan Geritz for valuable discussions. This research was supported by the Hungarian National Science Foundation (OTKA T 019272).

Evolutionary branching and coexistence of germination strategies

Andrea Mathias
Éva Kisdi

1. Introduction

Mixed strategies are often the best devices for adaptation to unpredictable, fluctuating environments (Levins 1962, 1968; Cohen 1966; Cooper and Kaplan 1982; Bull 1987; Philippi and Seger 1989; León 1993; Haccou and Iwasa 1995; Sasaki and Ellner 1995). Since population growth is a multiplicative process, the long-term fitness of a strategy in an (ergodic) stochastic environment is given by the geometric mean of its annual growth rates (Cohen 1966; Bulmer 1985; Metz *et al.* 1992). As the geometric mean is considerably decreased by occasional low values of the annual growth rate, avoiding years of poor recruitment is advantageous even at the cost of suboptimal performance in good years. Mixed strategies represent a genuine way to achieve this. Some individuals develop 'safe' phenotypes, which guarantee some recruitment even in very bad years, while other individuals produce ‘risky’ phenotypes ensuring high recruitment but only in good years. Although the mixture of 'safe' and 'risky' phenotypes has suboptimal recruitment in good years, it is buffered from extremely poor performance in bad years.

Germination behaviour of seeds of annual plants is a long-studied example of such mixed strategies (Cohen 1966; Bulmer 1984; Ellner 1985a,b, 1987; León 1985; Brown and Venable 1986; Klinkhamer *et al.* 1987; Venable and Brown 1988; Rees 1994). Annual plants take a high risk at germination in fluctuating environments, because they can loose their single reproductive opportunity if the environment turns out to be unsuitable for seedling establishment or reproduction. These plants can best insure themselves by keeping each year some seeds from germination, i.e., by developing a soil seed bank. Germination thus represents the 'risky' strategy, while dormant seeds are 'safe'. Indeed, delayed germination is common in annual plants living in risky environments like in deserts, during early successional phases and among weeds (Roberts and Feast 1973; Harper 1977; Ellner and Shmida 1981; Fenner 1985).

In his pioneering work, Cohen (1966) demonstrated the adaptive value of delayed germination in fluctuating environments and determined the optimal germination fraction assuming spatially homogeneous environment and density-independent (exponential) population growth. In density-dependent populations Ellner (1985a) showed that there is a unique global ESS for germination fraction (see also Bulmer 1984; Ellner 1985b). Ellner (1985a) also argued that in spatially homogeneous environments different germination strategies cannot coexist in an evolutionarily stable coalition, i.e., eventually the population will be monomorphic containing a single ESS germination fraction.

The evolution of germination fraction in spatially heterogeneous environments, however, is poorly understood. The few models addressing this problem assume that the environmental patches are stochastically equivalent, i.e., they represent merely different realizations of the same stochastic environmental process (Bulmer 1984; Klinkhamer *et al.* 1987; Venable and Brown 1988). Environmental heterogeneity affecting life history parameters (such as seed survival, yield, etc.), though ecologically plausible, has not been studied.

In this paper we set up a model which incorporates spatial heterogeneity of the latter type in addition to temporal fluctuations of the environment and density dependence. Since spatial heterogeneity and within-patch density dependence may promote coexistence of several strategies (cf. 'soft selection' models, Christiansen 1975; Strobeck 1979), we cannot rely merely on a traditional ESS-analysis of germination strategies.

There is a recently developed framework for modelling adaptive dynamics that accommodates coexisting strategies and gradual build-up of stable coalitions of strategies in initially monomorphic populations via evolutionary branching (Metz *et al.*1996; Geritz *et al.* 1997a,b; Geritz and Kisdi this volume). Using this modelling framework we show that different germination strategies may indeed coexist when the environment is spatially heterogeneous. No previous model predicted evolutionarily stable coexistence of different germination fractions. Moreover, we find evolutionary branching of germination strategy: An initially monomorphic population may become dimorphic containing two strategies with gradually more and more different germination fractions. The predictions of the model are confirmed by numerical simulations.

The finite-population simulations, however, revealed a specific evolutionary pattern which could not be predicted by the infinite-population model analysis. Due to environmental fluctuations, the density of one of the coexisting germination strategies may accidentally drop so much that the strategy goes extinct in a finite population. In this way the population falls back to monomorphism and starts to build up the evolutionarily stable coalition anew. Repeated events of extinction followed by evolutionary branching result in a cyclic evolutionary tree reminiscent of iterative evolution (Futuyma, 1998). We discuss how the modelling framework can be extended to incorporate extinction caused by environmental stochasticity in finite populations.

2. Model Assumptions

Consider an annual monocarp plant population having a seed bank, where a fraction G of the seeds germinates each year. We assume that the germination ability of seeds is independent of their age, i.e., the newly produced seeds have the same probability of germination at the beginning of the next reproductive period as the seeds which have been dormant (and are still viable) in the seed bank for several years. The environment in the soil is independent from the above-ground conditions, and can be characterised by a constant mortality rate, D, such that a fraction $(1-D)$ of the seeds survive until the next year.

The above-ground environment fluctuates in time. For simplicity we assume that there are only two types of years ('good' and 'bad'), and that years are uncorrelated. The distribution of the environment is thus specified by the probability of good years, p. The yield, Y, defined as the average number of seeds produced by one germinated seed, depends on the above-ground environment during the reproductive period and on population density. In bad years all seedlings die before reproduction, i.e., Y=0. In good years the yield is a decreasing function of the number of seedlings according to the "reciprocal yield law" (Harper 1977),

$$Y = y(GN) = \frac{a}{GN/\gamma + k} \tag{1}$$

where N is the number of seeds prior to germination, GN is therefore the number of competing seedlings, a and k are positive constants, and γ is the scaling factor of seed numbers (a higher value of γ results in proportionally higher seed numbers but does not change the annual or long-term growth rate). First we assume that γ is large enough for the population to be considered effectively infinite.

To model spatial heterogeneity we assume that the environment consists of two patches, which differ in the soil mortality rate of seeds (D_1 and D_2, respectively). The patches are identical otherwise: In particular, they experience good and bad years synchronously (unlike in the models of Bulmer 1984; Klinkhamer *et al.* 1987; Venable and Brown 1988). Density dependence operates within each patch independently; that is, the expected yield of a seedling depends on the number of seedlings in the same patch. Each year a fixed proportion of newly formed seeds, m, migrates to the other patch. Figure 1 summarizes the life cycle of the population.

Similar to traditional ESS analysis, we model germination strategies as if they were haploid, true-breeding genotypes. Mutations of germination fraction are assumed to be infrequent and to have small phenotypic effect.'

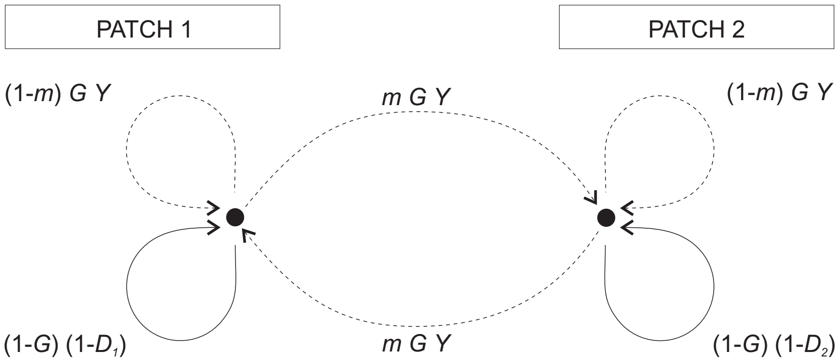

Figure 1. Life cycle diagram of a population of germination strategy G living in a spatially heterogeneous environment. Dashed lines: in good years only; solid lines: each year.

3. Invasibility Analysis

Assume the population is initially monomorphic for the resident strategy G. The number of seeds in patch 1 just prior to germination in year $t+1$, $N_G^{(1)}(t+1)$, is the sum of

(i) those seeds which were present in year t, did not germinate and survived in the soil, i.e., $(1-G)(1-D_1)N_G^{(1)}(t)$;

(ii) the non-migrant fraction of the yield produced by the seeds germinated in the previous year, $(1-m)y\left(GN_G^{(1)}(t)\right)GN_G^{(1)}(t)$, provided that year t was good; and

(iii) the seeds produced in the previous year in the other patch which migrated here, $my\left(GN_G^{(2)}(t)\right)GN_G^{(2)}(t)$, provided again that year t was good (cf. Figure 1). The number of seeds in the first and in the second patch thus follow the stochastic process

$$N_G^{(1)}(t+1)=\left\{\begin{array}{ll} N_G^{(1)}(t)\left[(1-G)(1-D_1)+(1-m)Gy\left(GN_G^{(1)}(t)\right)\right]+ & \\ +mN_G^{(2)}(t)Gy\left(GN_G^{(2)}(t)\right) & \text{if year } t \text{ is good} \\ & \\ N_G^{(1)}(t)\left[(1-G)(1-D_1)\right] & \text{if year } t \text{ is bad} \end{array}\right. \tag{2a}$$

and

$$N_G^{(2)}(t+1)=\left\{\begin{array}{ll} N_G^{(2)}(t)\left[(1-G)(1-D_2)+(1-m)Gy\left(GN_G^{(2)}(t)\right)\right]+ & \\ +mN_G^{(1)}(t)Gy\left(GN_G^{(1)}(t)\right) & \text{if year } t \text{ is good} \\ & \\ N_G^{(2)}(t)\left[(1-G)(1-D_2)\right] & \text{if year } t \text{ is bad} \end{array}\right. \tag{2b}$$

Strategy G is viable, i.e., it has a positive stationary distribution of seed numbers, if its long-term logarithmic growth rate at low population density is positive (Ellner 1985a). When population density is low, the yield in good years for both patches is approximately $y(0)=a/k$. Substitution of $y(0)$ into Eqs. (2) gives a density-independent stochastic matrix process, the long-term growth rate of which is hard to determine analytically (Tuljapurkar 1989). However, to obtain a sufficient condition for viability we can consider a population as if it lived only in the better patch (the one with lower mortality of seeds), and all migrant seeds were lost. The long-term logarithmic growth rate at low density of such a population would be $p \ln[(1-G)(1-D) + (1-m)\, G\, a/k] + (1-p) \ln[(1-G)(1-D)]$, where $D=\min(D_1\,;\,D_2)$ (cf. Cohen 1966). All strategies for which the above expression is positive are viable in the two-patch model of Eqs. (2) as well. In all examples presented below, the range of viable strategies is wider than (0.00011, 0.99999), i.e., practically all germination fractions are viable.

Now consider a rare mutant strategy, g, in the established population of strategy G. As long as the mutant density is negligible compared to the resident, the yield is determined by the number of seedlings of the resident strategy. The mutant's seed numbers in the next year therefore are

$$N_g^{(1)}(t+1)=\left\{\begin{array}{ll} N_g^{(1)}(t)\left[(1-g)(1-D_1)+(1-m)gy\left(GN_G^{(1)}(t)\right)\right]+ & \\ +mN_g^{(2)}(t)gy\left(GN_G^{(2)}(t)\right) & \text{if year } t \text{ is good} \\ & \\ N_g^{(1)}(t)\left[(1-g)(1-D_1)\right] & \text{if year } t \text{ is bad} \end{array}\right. \tag{3a}$$

and

$$N_g^{(2)}(t+1)=\begin{cases} N_g^{(2)}(t)\left[(1-g)(1-D_2)+(1-m)g\,y\left(GN_g^{(2)}(t)\right)\right]+ & \\ +mN_g^{(1)}(t)g\,y\left(GN_G^{(1)}(t)\right) & \text{if year } t \text{ is good} \\ & \\ N_g^{(2)}(t)\left[(1-g)(1-D_2)\right] & \text{if year } t \text{ is bad} \end{cases} \tag{3b}$$

The mutant strategy will spread if its long-term logarithmic growth rate is positive. Unfortunately, the long-term growth rate of the mutant cannot be obtained analytically since (i) it depends on the unknown distribution of the resident seed numbers, $N_G^{(1)}(t)$ and $N_G^{(2)}(t)$, and (ii) the calculation of the long-term growth rate in structured populations is cumbersome even if the resident distribution were known.

In order to get a numerical approximation for the mutant long-term growth rate, we simulated the resident population dynamics (Eqs. (2)) and sampled the stationary distribution of the resident seed numbers. Iterating Eqs. (3) we calculated the annual growth rate of the rare mutant in each year *t*,

$$\frac{N_g(t+1)}{N_g\ (t)} \tag{4}$$

where $N_g(t)=N_g^{(1)}(t)+N_g^{(2)}(t)$ is the total number of seeds of the mutant strategy. The long-term logarithmic growth rate of the mutant strategy g in the resident population G is

$$r(g,G)=\frac{1}{T}\sum_{t=0}^{t=T-1}\ln\frac{N_g(t+1)}{N_g(t)} \tag{5}$$

(Cohen 1966; Bulmer 1985; Metz *et al.* 1992). If *r* (*g,G*) is positive then the mutant strategy is able to invade the resident, otherwise the mutant dies out.

4. Adaptive dynamics of germination strategies

Repeating the invasibility analysis for many pairs of (viable) mutant and resident strategies we determined which mutant strategies can invade given resident populations. The results are summarized by a so-called pairwise invasibility plot, i.e., a sign plot of *r*(*g,G*) (Van Tienderen and De Jong 1986; Metz *et al.* 1992; Kisdi and Meszéna 1993, 1995; Geritz *et al.* 1997a,b). Figures 2a and 3a show pairwise invasibility plots for two sets of parameter values. Below we summarize the information obtained from the model analysis; see Metz *et al.* (1996), Geritz *et al.*(1997a,b), or Geritz and Kisdi (this volume) for a detailed account on the applied methods.

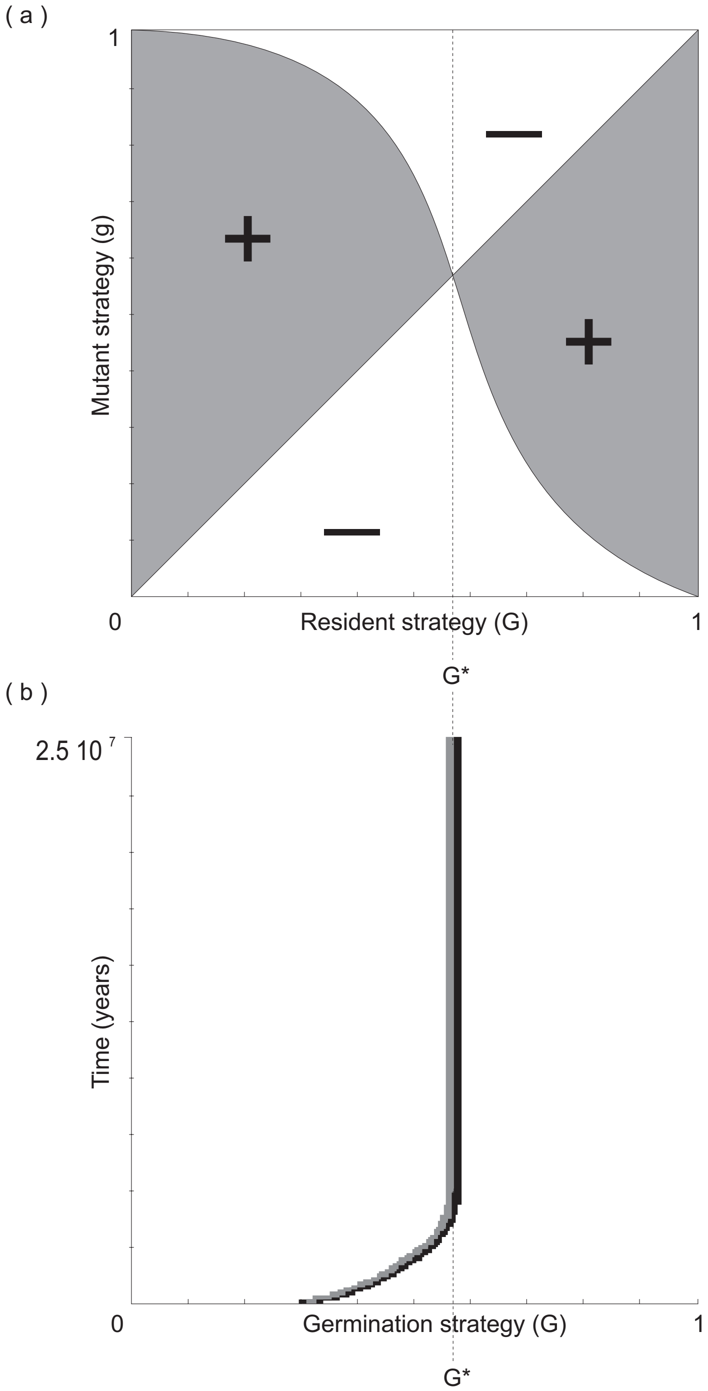

Figure 2. (a) Pairwise invasibility plot with an evolutionarily stable germination strategy G^*=0.57. Model parameters: m=0.2, D_1 =0.1, D_2 =0.9, p=0.7, $a=5\cdot10^3$, k=3, γ=100. (b) Simulated evolutionarily tree.

In the first example (Figure 2a) there is a germination fraction, G^*=0.57, which is evolutionarily stable: No mutant strategy g has a positive long-term growth rate in the established population of G^*. Moreover, G^* is a convergence stable strategy. If the initial germination fraction is smaller than G^*, then a mutant with slightly higher germination fraction can invade and vice versa, therefore the germination fraction converges towards G^* via small mutational steps (Eshel and Motro 1981; Eshel 1983;

Taylor 1989; Christiansen 1991). The population thus undergoes directional evolution until the ESS germination fraction is established.

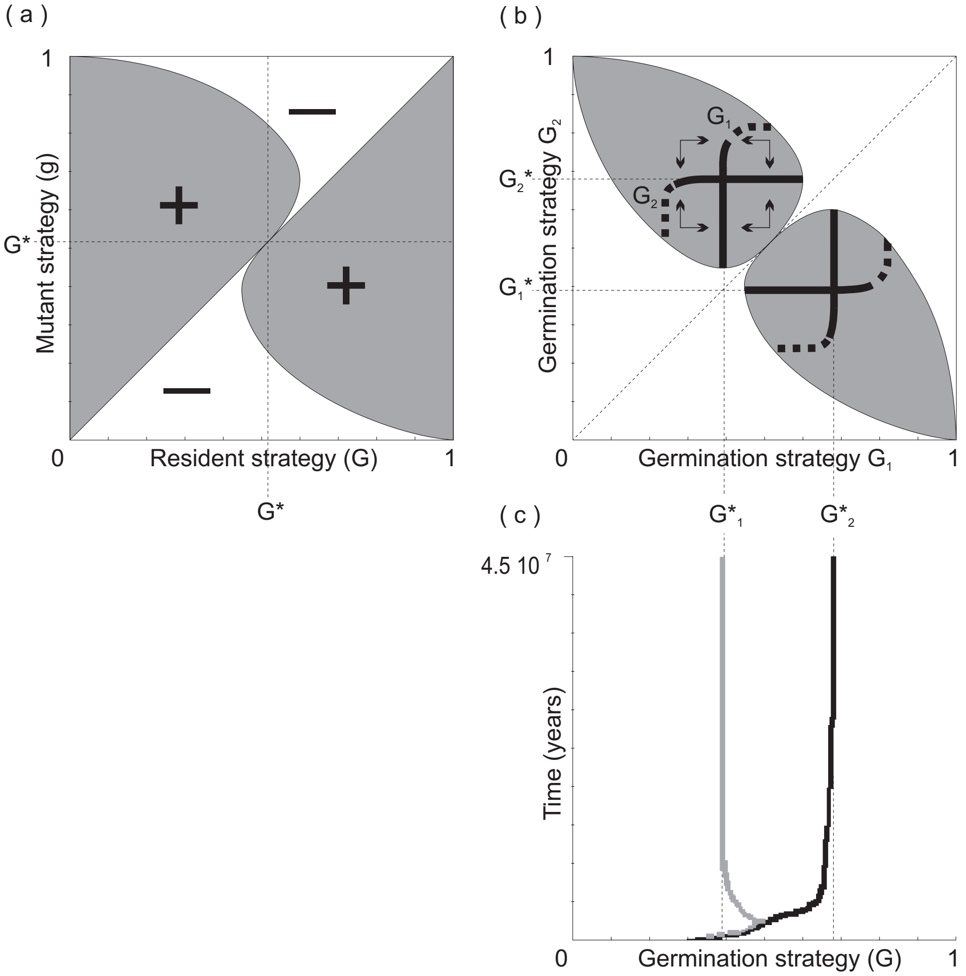

Figure 3. (a) Pairwise invasibility plot with a branching point at G*=0.52. Model parameters: m=0.01, D_1=0.1, D_2=0.9, p=0.7, a=$5\cdot10^3$, k=3, γ=$2\cdot10^8$.

(b) Isocline plot. Shaded areas: set of strategy pairs which can coexist in protected dimorphisms; arrows: directions of evolution in G_1 (horizontal) and G_2 (vertical). Thick lines: G_1 and G_2 isoclines; solid: evolutionarily stable, dashed: evolutionarily unstable. The symmetry of the plot on its main diagonal is the consequence of the interchangeable notation of G_1 and G_2.

(c) Branching of the evolutionary tree and directional evolution towards the evolutionarily stable dimorphism. Grey and black colored points represent the strategies, which are more frequent in the first and in the second patch, respectively.

In the second example (Figure 3a), the germination fraction G^*=0.52 is convergence stable but not evolutionarily stable: It represents a unique configuration called evolutionary branching point. Notice that any mutant strategy sufficiently close to G^*, either larger or smaller, can invade the resident population of G^*, but G^* as a rare mutant can also invade any other strategy. In the vicinity of G^* therefore the population will become dimorphic, containing two very similar germination strategies, the original resident and a slightly different mutant. Once the population has become dimorphic, the coexisting strategies undergo divergent coevolution resulting in two clearly distinct germination fractions. The evolutionary tree of germination strategies thus develops two branches.

Modelling evolution after evolutionary branching requires determining the set of strategy pairs, which can form a protected dimorphism (the dimorphic counterpart of the concept of viable strategies in monomorphic populations, cf. Metz *et al.* 1996), and finding the evolutionarily stable dimorphism in this set. Those strategies can coexist in protected dimorphism, which can invade each other's population when rare. The set of possible dimorphisms therefore can be obtained by mirroring the pairwise invasibility plot along its main diagonal, and comparing the mirror image to the original: The overlapping parts of the 'invasion' areas contain the pairs of strategies which are able to coexist (Figure 3b).

A dimorphic population may be invadable by a third mutant strategy. To see whether a mutant strategy, g, can invade a dimorphic resident population of G_1 and G_2, we must calculate its long-term growth rate, r (g, G_1 ,G_2,). Analogously to Eqs. (3), the mutant's seed numbers in the two patches in the next year are

$$N_g^{(1)}(t+1)=\begin{cases} N_g^{(1)}(t)\left[(1-g)(1-D_1)+(1-m)g\,y\left(G_1N_{G_1}^{(1)}(t)+G_2N_{G_2}^{(1)}(t)\right)\right]+ \\ +mN_g^{(2)}(t)g\,y\left(G_1N_{G_1}^{(2)}(t)+G_2N_{G_2}^{(2)}(t)\right) \qquad \text{if year } t \text{ is good} \\ \\ N_g^{(1)}(t)\left[(1-g)(1-D_1)\right] \qquad \text{if year } t \text{ is bad} \end{cases} \tag{6a}$$

and

$$N_g^{(2)}(t+1)=\begin{cases} N_g^{(2)}(t)\left[(1-g)(1-D_2)+(1-m)g\,y\left(G_1N_{G_1}^{(2)}(t)+G_2N_{G_2}^{(2)}(t)\right)\right]+ \\ +mN_g^{(1)}(t)g\,y\left(G_1N_{G_1}^{(1)}(t)+G_2N_{G_2}^{(1)}(t)\right) \qquad \text{if year } t \text{ is good} \\ \\ N_g^{(2)}(t)\left[(1-g)(1-D_2)\right] \qquad \text{if year } t \text{ is bad} \end{cases} \tag{6b}$$

where $N_{G_1}^{(1)}(t)$, $N_{G_1}^{(2)}(t)$, $N_{G_2}^{(1)}(t)$ and $N_{G_2}^{(2)}(t)$ denote the number of seeds of the resident strategies in the two patches. The population dynamical equations for the two resident strategies can be obtained from Eqs. (6) by substituting G_1 and G_2 for g, respectively. Similarly to the monomorphic case, we simulated the resident dimorphic population and estimated r (g,G_1, G_2) numerically (cf. Eqs. (4) and (5)).

In order to find the evolutionarily stable dimorphism, consider the following thought experiment. Assume that one of the resident strategies, say G_1, is fixed, while G_2 is allowed to evolve. The mutant long-term growth rate, r (g,G_1,G_2), thus can be recast as r_1(g,G_2) with G_1 as a parameter, and analysed by a pairwise invasibility plot. The ESSs or branching points of G_2 for different fixed values of G_1 constitute the so-called G_2-isocline (Figure 3b). The G_1-isocline is constructed analogously.

The horizontal (vertical) arrows on Figure 3b show the direction of evolution of G_1 (G_2) in the dimorphic population. As the arrows indicate, directional evolution converges to the intersection of the G_1 - and G_2 -isoclines (see Matessi and Di Pasquale 1996). The intersection of the isoclines corresponds to a pair of strategies both of which are evolutionarily stable given the value of the other: These strategies form the evolutionarily stable dimorphism. Following evolutionary branching, the population is thus expected to evolve to the evolutionarily stable dimorphism where evolution comes to a halt.

5. Simulation of the evolutionary tree

The predicted course of evolution can be compared to direct simulation. Figures 2b and 3c show the simulated evolutionary trees for the two examples shown above. We start with an arbitrary monomorphic population (G=0.3) and simulate the sequence of seed numbers in consecutive years (Eqs. 2). Mutant strategies are periodically generated by small mutational step (ΔG=0.0025) in random directions from the strategy (or strategies) already present, and introduced into the population at low initial density ($N_g^{(1)} = N_g^{(2)} = 1$).We then continue to simulate the joint population dynamics of all strategies present. If the seed number of a strategy drops below one, then it is considered extinct and removed from the population. Demographic stochasticity of rare mutants was not taken into account during the simulations. On the figures, we plot the strategies present as a function of time.

In the first example (Figure 2b), strategies with higher germination fraction spread in the population, and lower germination fractions are purged. Germination fraction thus gradually increases until it arrives at the ESS value G*=0.57, as predicted by the pairwise invasibility plot (Figure 2a).

In the second example the pairwise invasibility plot (Figure 3a) indicates directional evolution to G*=0.52 and evolutionary branching in the neighbourhood of G*. According to the isocline plot (Figure 3b), the two germination strategies coevolve to the evolutionarily stable dimorphism at $G_1 = 0.39$ and G_2 =0.68. Indeed, the simulated evolutionary tree (Figure 3c) shows that germination fraction first increases towards the branching point, G*. As the population approaches G*, variation builds up in germination fraction on both sides of G*, and strategies in the middle go extinct. The emerging branches evolve apart and converge to the predicted evolutionarily stable dimorphism. The number of individuals with low germination fraction is higher in the first patch than in the second: In the first patch seed mortality is low and therefore dormant seeds are safe. Most individuals of the high germination strategy are in the second patch, where seed mortality is high.

6. Cycles of evolutionary branching and extinction in finite populations

So far we have assumed that a strategy is protected from extinction if its long-term growth rate is positive when rare. The number of seeds, however, fluctuates widely: In good years the population quickly grows towards a saturation density but in bad years the number of seeds decreases exponentially. In finite populations these fluctuations can occasionally lead to very small population numbers and therefore to extinction.

In order to assess which strategies can coexist for a given length of time in a finite population, we run a series of simulations iterating Eqs. 6 for a number of pairs of resident strategies. To avoid the intricacies of demographic stochasticity at low population numbers, we simply considered a strategy extinct if its total seed number was below 1. From the repeated simulations we estimated the expected time until extinction of one strategy in the stationary stochastic process of seed numbers of the given strategy pair. The results of these simulations for two different population sizes are shown in Figures 4a and 5a.

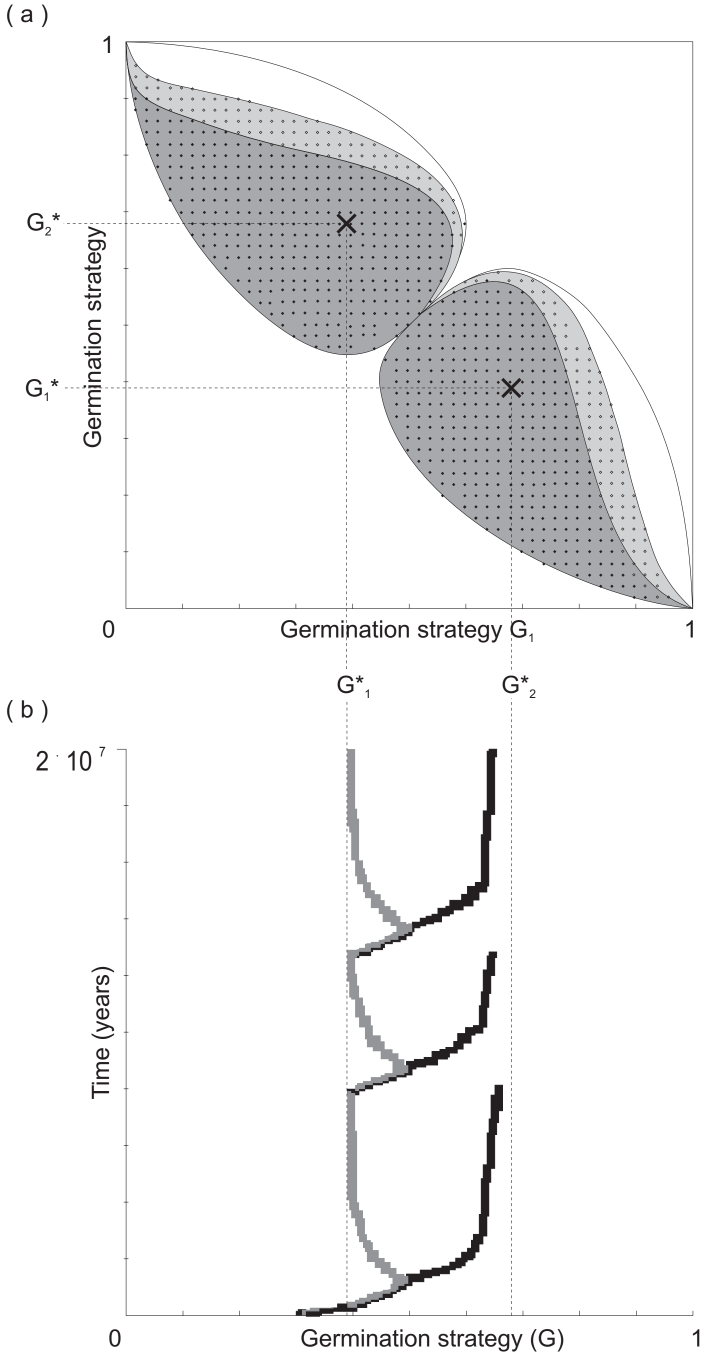

Fig 4. (a) Expected time of coexistence for strategy pairs in the area of protected dimorphisms. Area marked dark gray: average time until extinction of one strategy of the dimorphism is higher than 10^4 years, light grey: average time until extinction is between 10^3 and 10^4, white: average time until extinction is less than 10^3. X-marks: the evolutionarily stable dimorphism. Model parameters: m=0.01, D_1 =0.1, D_2 =0.9, p=0.7, a=5·10^3, k=3, γ=2·10^4 . Average times were estimated from 50 simulations.

(b) Simulated evolutionary tree with cyclical extinction and branching. Coevolution approaches the evolutionarily stable dimorphism; extinction of the larger germination strategy is followed by repeated branching.

In a considerable part of the set of protected dimorphisms one strategy can go extinct in relatively short time compared to the evolutionary time scale, therefore a protected dimorphism indeed does not guarantee long-term coexistence in finite populations. Extinction occurs when a sufficient number of bad years come in a series. High germination fraction strategies are especially doomed to extinction, since their seed number decreases fast during bad years. Since the critical number of bad years is greater if the population is large, and a longer series occurs with lower probability, the expected time until extinction increases with population size, especially strongly when bad years are rare. Population size is set by the scaling factor γ (Eqs. 1). In biological terms, $a\gamma$ corresponds to the saturation amount of crop produced by the whole population in a good year if the number of competing seedlings is very high, i.e., $a\gamma$ is the 'carrying capacity' for the standing crop. Figure 4a shows the expected time until extinction in a large population with $a\gamma = 10^8$. Extinction times are considerably shorter in a small population with $a\gamma = 10^4$ (Figure 5a).

If one strategy of a dimorphism goes extinct, the population falls back to monomorphism. The monomorphic population evolves back to the branching point, undergoes evolutionary branching and evolves towards the evolutionarily stable dimorphism until extinction happens again. The evolutionary tree thus shows cycles of branching and extinction (Figures 4b and 5b). In a large population (Figure 4b), evolution from the branching point to the evolutionarily stable dimorphism passes through strategy pairs which can coexist for long time. The population thus approaches the evolutionarily stable dimorphism and spends considerable time nearby before extinction of the upper branch. In a small population (Figure 5b), however, the evolutionarily stable dimorphism cannot persist for a long time. Moreover, the expected time until extinction is also small for the strategy pairs encountered during coevolution towards the evolutionarily stable dimorphism. The upper branch of the evolutionary tree goes extinct much before coevolution would reach the evolutionarily stable dimorphism. The pattern of the evolutionary tree also depends on the frequency and size of mutations: More frequent or larger mutations speed up evolution, hence the probability of extinction before reaching the evolutionarily stable coalition decreases. Notice that γ was set at a very high value in the example of section 4, therefore extinction did not occur during the simulation depicted on Figure 3c.

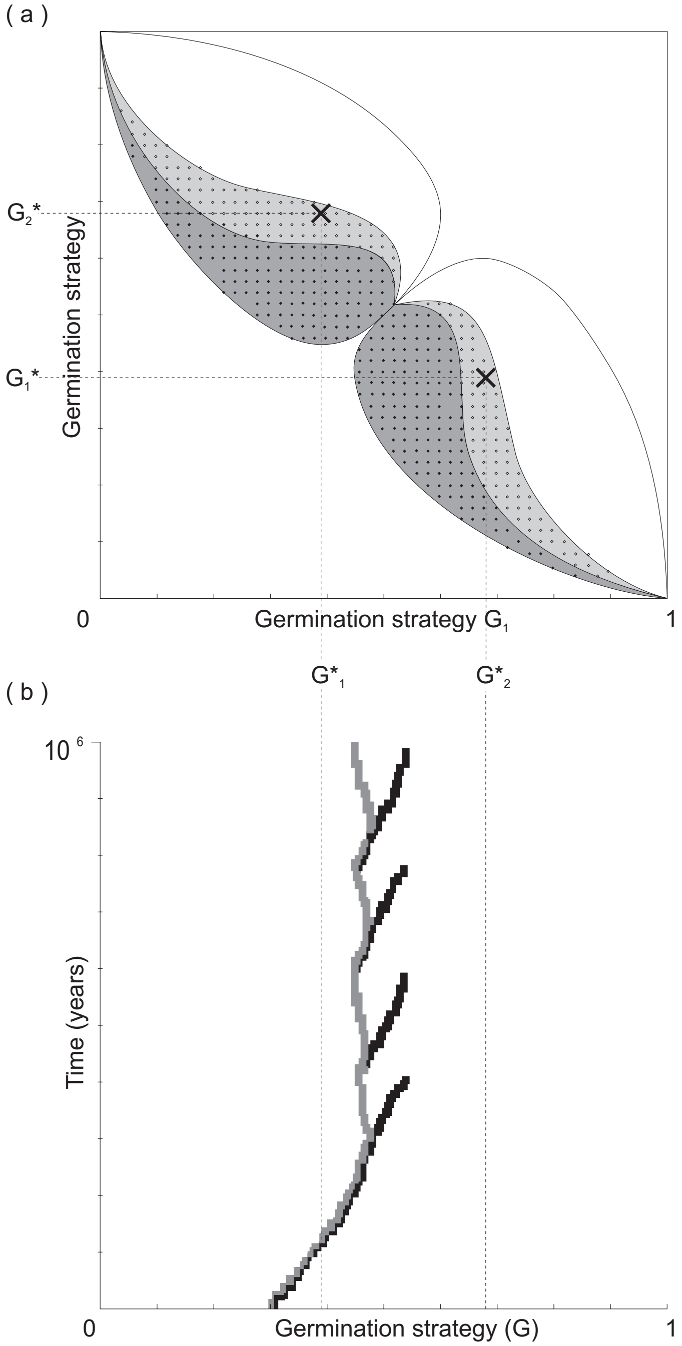

Figure 5. (a) Expected time of coexistence for strategy pairs in the area of protected dimorphisms. Area marked black: average time until extinction of one strategy of the dimorphism is higher than 10^4 years, grey: average time until extinction is between 10^3 and 10^4, white: average time until extinction is less than 10^3. X-marks: the evolutionarily stable dimorphism. Model parameters: m=0.01, D_1=0.1, D_2=0.9, p=0.7, a=5·10^3, k=3, γ=2. Average times were estimated from 50 simulations.

(b) Simulated evolutionary tree with cyclical extinction and branching. Extinction happens before coevolution could approach the evolutionarily stable dimorphism.

7. Discussion

In the present paper we have shown that several strategies with different germination fractions can coexist, and form an evolutionarily stable coalition. Assuming small mutations, the evolutionarily stable coalition can be built up in an initially monomorphic population by evolutionary branching. The monomorphic population first evolves towards a germination fraction at which the long-term growth rate is actually minimal (Geritz 1997a; see also Abrams *et al.* 1993). In the neighbourhood of this so-called branching point even very similar strategies can coexist, i.e., a dimorphism is feasible by a small mutational step. Once the population has become dimorphic, the two strategies gradually evolve away from each other and approach the evolutionarily stable coalition of two distinct germination strategies. The evolutionarily stable coalition of mixed strategies is stable not only against perturbations in population numbers but also against invasion by any new mutant strategy.

In finite populations, however, a strategy can go extinct due to the fluctuations in population numbers even if it is viable in an infinite population, i.e., if its long-term growth rate is positive when rare. After extinction of one strategy of the dimorphic coalition, the remaining monomorphic population evolves back to the same branching point where it became dimorphic in the first place. Extinction is thus followed by evolutionary branching again in repeated cycles.

Key components of the model

Modelling the evolution of germination fraction naturally presumes that germination fraction is under genetic control and therefore can be subject to selection. Between-year innate dormancy (i.e., the inability to germinate even when environmental conditions are suitable for germination) seems to be to a large extent determined by the mother plant, for example by an impermeable seed coat or chemical inhibitors (Harper 1977; Ellner and Shmida 1981; Westoby 1981; Mayer and Poljakoff-Mayber 1982; Ellner 1986). Substantial variation in germination fraction occurs between seeds of different individuals (El-Kassaby *et al.* 1992; Giannini and Bellari 1995). Germination fraction also varies between populations (e.g. Sorensen 1993; Giannini and Bellari 1995), possibly indicating adaptation to the local environmental conditions. Evolution of germination has occurred during the process of domestication of many commercial crops: Although their wild ancestors have dormant seeds, the seeds of the cultivated forms germinate immediately (Harper 1977). Many plant species, especially weeds, exhibit somatic polymorphism within a mother plant in requirements for breaking dormancy (often associated to seed size polymorphism or to the position of the seed on the plant). By changing the proportions of the different seed morphs, germination fraction of the seeds can be varied. For example, the disc and ray florets of many Compositae produce different achenes (one-seeded dry fruits), which highly differ in germination fraction (Forsyth and Brown 1982). The ratio between the floret types can be changed by selection (Harper 1977), which consequently changes the overall germination fraction as well.

In the present model we assumed temporal fluctuations of the environment, spatial heterogeneity, and density dependence. It is only the combined effect of all these three mechanisms that leads to evolutionary branching and evolutionarily stable coalitions of germination fractions. In a spatially homogeneous population with no density dependence the annual growth rate of a germination strategy depends only on the actual state of the fluctuating environment, therefore the long-term growth rate of each strategy is determined once the distribution of the environment is specified. Finding the optimal germination fraction then simply amounts to the maximization of the long-term growth rate (Cohen 1966). This basic result can be generalized to spatially heterogeneous populations straightforwardly. If the environment consists of a number of patches, the population is characterized by a vector containing seed numbers in different patches. The population dynamics can be described by stochastic projection matrices, the matrix entries being determined by the within-patch dynamical parameters and the between-patch migration rates. The theory of stochastic projection matrices (reviewed by Caswell 1989 and Tuljapurkar 1989) shows that there is a well-defined long-term growth rate attached to each germination strategy, and the strategy having the largest growth rate eventually outnumbers all others. Although spatial heterogeneity makes the calculation of the long-term growth rate much harder, it does not affect the conclusion of a single optimal ger

Including density dependence changes the problem significantly. If the environment fluctuates, then population density (or any other relevant measure of intraspecific competition) fluctuates as well. The long-term growth rate of a strategy is determined by the joined distribution of the environment and density. As the density distribution is generated by the resident population, the long-term fitness of a mutant depends on the resident strategy (or strategies). Selection thus becomes frequency dependent (Kisdi and Meszéna 1993, 1995). Still in the particular case of germination fraction there is always a single global ESS if the environment is spatially homogeneous (Bulmer 1984; Ellner 1985a). Including spatial heterogeneity makes evolutionary branching and evolutionarily stable coalitions possible.

In order to get evolutionary branching and evolution of two germination fractions, migration between the patches must be small: In case of moderate and high migration a generalist ESS outcompetes all other strategies (cf. Figure 2). Assuming small migration between the patches, however, does not mean assuming two evolutionarily independent populations. In absence of one strategy, as after extinction, the other strategy undergoes fast evolution towards the branching point (cf. Figure 4b).

Small migration is obviously ensured if there is some barrier between the patches such as physical distance. Migration can also be subject to evolution, and a number of mechanisms may influence whether higher or lower levels of migration are selected for. Migration is beneficial when the fluctuating environmental effects are not perfectly correlated across the patches and thus bad years can be avoided by dispersal (Levin *et al.* 1984; Klinkhamer *et al.* 1987; Venable and Brown 1988; Cohen and Levin 1991) or if seedlings from nondispersed seeds experience strong competition with their sibs (Geritz *et al.* 1984). On the other hand, migration is often costly: For example, structures need to be developed in order to facilitate dispersal (like nutritious fruits for endozoochory), dispersal may require small seed size which can be disadvantageous for seedling survival (Harper 1977), or dispersed seeds may be lost if ending up in unsuitable habitats. If the costs outweigh the potential benefits, then migration is expected to decrease during evolution. Once migration is small enough evolutionary branching to occur, an evolutionarily stable coalition of germination strategies will evolve, where each strategy is better adapted in one patch and less adapted in the other patch. This strengthens selection for even smaller migration (Balkau and Feldman 1973), which may eventually lead to parapatric speciation.

Coexistence and evolutionary branching of mixed strategies

Prevalence of a single mixed strategy on the one hand, and coexistence of several pure strategies on the other hand is often thought as two complementary possibilities for the outcome of evolution. In linear games coexistence of mixed strategies is neutral as long as their mixture yields the same evolutionarily stable population strategy (Thomas 1984). In fluctuating environments, however, a monomorphic population of a mixed strategy markedly differs from a coalition of pure or mixed strategists (cf. Bulmer 1984). From a mathematical point of view this is so because the long-term growth rate is a nonlinear function of the mutant's strategy. Intuitively, the reason is the following. In a population of a single mixed strategy the frequencies of pure strategies are constant in time, determined by the genotype. When several pure (or mixed) strategists coexist, however, then the frequencies fluctuate as consecutive years favor different strategies over the others. Note that in the present model (like in a model of Cohen 1966) the pure strategies are not even viable: The always germinating strategy (G=1) disappears in the first bad year when there is no yield at all, while the always dormant strategy (G=0) is doomed to extinction in the soil. As coalitions of mixed strategies are not equivalent to each other or to single mixed strategies in fluctuating environments, the evolutionarily stable coalition is a unique outcome of evolution, which cannot be replaced by any single mixed strategy.

Evolutionary branching or evolutionarily stable coalitions of pure strategies chosen from a continuous strategy set have been found in constant environment models which assume spatial heterogeneity and density dependence operating within the patches (i.e., 'soft selection'; Brown and Pavlovic 1992; Meszéna *et al.* 1997; Geritz *et al.* 1997a; Geritz and Kisdi this volume; Kisdi and Geritz *in prep.*) or which assume some other frequency-dependent selection mechanism (Brown and Vincent 1987, 1992; Metz *et al.* 1992; Taper and Case 1992; Geritz *et al., in prep.*). Evolutionarily stable coalitions in case of mixed strategies, however, have been previously reported only by Ludwig and Levin (1991). They found that two dispersal types characterized by different ratio of dispersed:nondispersed seeds form an evolutionarily stable coalition, although one strategy of this coalition was always the pure all-dispersing type.

Cyclical extinction and evolutionary branching in finite populations

In finite populations, protected polymorphism does not guarantee the persistence of a coalition in fluctuating environments. The population number of a strategy may fluctuate widely, and occasionally may reach zero even if the strategy has a positive long-term growth rate when rare. Demographic stochasticity and Allee-effects will further increase the probability of extinction of a strategy present in small number.

The set of possible strategy coalitions should thus be redefined such that it reflects persistence of all constituent strategies with a given probability for a given time. As a first attempt, we considered the expected time until extinction of a strategy for each dimorphic population. This measure must be used with caution because the distribution of extinction times under environmental stochasticity is skewed (cf. Strebel 1985).

In conservation biology, the most often used concept to characterize persistence is the minimal viable population size (or MVP), i.e., the equilibrium size of the population required in absence of environmental stochasticity to ensure persistence when stochasticity is added (e.g. Goodman 1987; Nunney and Campbell 1993). The concept of MVP could be generalized such that a strategy coalition is considered persistent if all its strategies have sufficiently high equilibrium densities without stochasticity. However, this generalized MVP cannot be defined if environmental stochasticity is not merely a noise to remove but essential for maintaining the coalition (cf. Chesson 1986). In the present model, for example, only the highest germination rate would remain in a constant environment; therefore coalitions cannot be characterized by the equilibrium densities of their strategies.

When the evolutionarily attractor of the dimorphic population is outside of the set of persistent dimorphisms, one of the branches of the evolutionary tree goes extinct. Evolution leading to extinction of one (or several) strategies was also found for example by Taper and Case (1992), Matsuda and Abrams (1994a,b), Dieckmann *et al.* (1995), Law *et al.* (1997), and Geritz *et al.*(*in prep.*). However, in these models the remaining population never evolved back to the branching point, and therefore no cyclic evolutionary tree was found.

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