Adaptive diversification of germination strategies

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Evolution of the germination rate (the proportion of newly produced and dormant seeds that germinates every year) of annual plants is investigated, when the environment is temporally stochastic and spatially heterogeneous. The environment consists of two habitats with synchronous stochastic variation in the annual yield and permanent difference in constant seed survival rates. Density dependence operates within the habitats, which are connected via restricted seed dispersal. We find that instead of a single common evolutionarily stable strategy the coexistence of several germination strategies is possible and that in an initially monomorphic population evolutionary branching may occur. During evolutionary branching the population undergoes disruptive selection and splits into two branches of different lineages that converge to the evolutionarily stable coalition of different germination strategies. It is shown that spatial heterogeneity and restricted dispersal are essential for evolutionary branching. Disruptive selection on the germination rate presents yet another possibility for parapatric speciation.

Keywords: dormancy; stochastic environment; spatial heterogeneity; mixed strategy; evolutionary branching; adaptive dynamics

1. INTRODUCTION

In stochastic environments long-term fitness is given by the geometric mean of the annual growth rate (Cohen 1966; Bulmer 1985; Metz *et al.* 1992). Since the geometric mean is considerably decreased by occasional low values of the annual growth rate, it is advantageous to avoid very low levels of recruitment in bad years even at the cost of suboptimal performance in good years. Mixed strategies represent an ingenious way of reducing the risk of low recruitment (Levins 1962; Cohen 1966; Philippi & Seger 1989; León 1993; Haccou & Iwasa 1995; Sasaki & Ellner 1995). Delayed germination of seeds is a much-studied mixed strategy that serves as a risk-spreading mechanism when successful seed establishment is uncertain (Cohen 1966; Bulmer 1984; Ellner 1985a,b, 1987; Brown & Venable 1986; Klinkhamer *et al.* 1987; Venable & Brown 1988; Rees 1994). In fluctuating environments, annual plants take high risk with full germination, because they can lose their single reproductive opportunity in unsuitable years. These plants can best insure themselves by each year preventing a small amount of seeds from germinating, i.e. by developing a soil seed bank. Dormant seeds represent a 'safe' strategy and guarantee a constant opportunity of recruitment even in bad years; germination is the 'risky' strategy, giving high levels of recruitment but only in good years. Although the mixture of 'safe' and 'risky' phenotypes is suboptimal in good years, it buffers the population from extremely poor performance in bad years. Delayed seed germination is indeed common in annual plants living in risky environments; examples include deserts and early successional phases (Roberts & Feast 1973; Harper 1977; Ellner & 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 a spatially homogeneous environment and density-independent (exponential) population growth. In density-dependent populations Ellner (1985a) showed that there is a unique global evolutionarily stable strategy (ESS) 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 would be monomorphic containing only one ESS germination fraction.

The evolution of the germination fraction in spatially heterogeneous environments is, however, 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 & Brown 1988). Permanent environmental heterogeneity affecting life-history parameters (such as seed survival, yield, etc.), though ecologically plausible, has not been studied.

In addition to local density dependence and temporal fluctuations in yield, our model incorporates permanent spatial heterogeneity in seed survival. Spatial heterogeneity and within-patch density dependence may promote the coexistence of several strategies (cf. 'soft selection' models, Christiansen 1975; Strobeck 1979) and thus we cannot rely merely on traditional ESS analysis, which is unsuitable for studying evolution in polymorphic populations. Using the adaptive dynamics framework of Metz *et al.* (1996) and Geritz *et al.* (1997, 1998) we find that by evolutionary branching an initially monomorphic population may become dimorphic with gradually diverging germination strategies, and that different germination strategies may coexist in an evolutionarily stable coalition. Next we perform a bifurcation analysis to determine the

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range of model parameters that allows the evolutionary branching of germination strategies.

2. THE MODEL

An annual monocarpic plant with a seed bank is considered. Each year a fraction, G , of the seeds germinates. The above-ground conditions fluctuate over time and for simplicity we assume independent years and only two environmental states such that in ‘good’ years (that occur with probability p) plants produce yield but in ‘bad’ years all plants fail to reproduce. The population occupies two habitats that differ in the survival rates of dormant seeds (s_1 and s_2 , respectively). The two habitats experience synchronous above-ground fluctuations and are connected to each other such that a fraction D of new seeds disperses each year to the other habitat. Thus the number of seeds before germination in habitat 1 and habitat 2, respectively, changes from year to year according to

$$N_1(t+1) = (1-G)s_1N_1(t) + G(1-D)Y_1(t)N_1(t) + GDY_2(t)N_2(t), \quad (2.1a)$$

$$N_2(t+1) = (1-G)s_2N_2(t) + G(1-D)Y_2(t)N_2(t) + GDY_1(t)N_1(t), \quad (2.1b)$$

where the per capita yield $Y_i(t)$ ($i=1,2$) depends on local plant density and on the current environment, i.e.

$$Y_i(t) = \begin{cases} \frac{k}{GN_i(t) + a} & \text{if year } t \text{ is good} \\ 0 & \text{if year } t \text{ is bad} \end{cases} \quad (2.2)$$

where $GN_i(t)$ is the number of competing seedlings in the i th habitat in year t and a and k are positive constants.

A mutant germination strategy g can invade a resident population with strategy G if its long-term logarithmic growth rate, $r(g, G)$, is positive (Metz *et al.* 1992, 1996). Unfortunately, the growth rate cannot be obtained analytically. We simulated the population dynamics of the resident's strategy to determine the stationary distribution of plant density ($N_i(t)$) and therefore of yield ($Y_i(t)$); next we simulated the mutant's dynamics and estimated the growth rate numerically.

Figure 1a shows the pairwise invasibility plot (the sign plot of $r(g, G)$, Van Tienderen & de Jong (1986); Metz *et al.* (1996); Geritz *et al.* (1998)) for one particular set of parameters (s_1, s_2, D, a, k, p). Assuming small mutations (i.e. that $|g - G|$ is small), mutants that are nearer to the strategy of $G^* = 0.52$ can invade the former resident. By repeated invasions and substitutions, evolution converges to G^* (Eshel 1983; Christiansen 1991). However, G^* lacks evolutionary stability in the sense that it is not resistant to invasions of rare mutants (Maynard Smith 1982). Convergence stable (i.e. locally attracting) but evolutionarily unstable one-dimensional strategies are evolutionary branching points (Geritz *et al.* 1998): close to G^* , the population becomes dimorphic and the two coexisting strategies undergo divergent coevolution.

Evolution in dimorphic populations is modelled analogously to the monomorphic case (Geritz *et al.* 1998). For the resident-population dynamics equations (2.1) are applied to both residents with their respective germination

Figure 1. (a) Pairwise invasibility plot with a branching point at $G^* = 0.52$. Shaded areas, mutants can invade (positive fitness); white areas, mutants die out (negative fitness). (b) Evolution in a dimorphic population. Shaded areas, set of strategy pairs (G_1, G_2) that coexist in a protected dimorphism. The symmetry of the plot on its main diagonal is the consequence of the interchangeable notation of G_1 and G_2 . Arrows indicate the directions of the evolution of G_1 (horizontal) and G_2 (vertical). The G_1 and G_2 germination rates evolve towards the strategies indicated by thick curves. These strategies are evolutionarily stable (solid) or evolutionarily unstable (dashed). The final resting point of the dimorphic evolution is at the intersection of the thick curves, which corresponds to the evolutionarily stable coalition of $G_1^* = 0.39$ and $G_2^* = 0.68$. (c) Branching of the evolutionary tree and directional evolution towards the evolutionarily stable dimorphism. Model parameters: $D = 0.01$, $s_1 = 0.9$, $s_2 = 0.1$, $p = 0.7$, $k = 10^4$, $a = 4$.

strategies and with a per capita yield that depends on the sum of the local plant densities. The direction of evolution of each resident is deduced from the growth rates of their mutants and is indicated by arrows in figure 1b. Dimorphic evolution converges to a state where the germination strategies $(G_1^*, G_2^*) = (0.39, 0.68)$ coexist in an evolutionarily stable coalition (see Matessi & Di Pasquale (1996) for dimorphic convergence).

Direct simulation of the evolutionary process (figure 1c) confirms the scenario deduced from the adaptive dynamics. In the simulation we introduced new mutants that differ from one of the residents by a small mutational step of 0.0025 at a small initial number (10^{-8}) in each habitat, simulated the joint population dynamics of all strategies present, and each year we removed the strategies the density of which fell under the initial value (10^{-8}). Demographic stochasticity of rare strategies was neglected. This simulation also reveals that in dimorphic populations the strategies are associated with the habitats—plants with a low-germination-rate strategy mainly occur in the habitat where seed mortality is low, whereas plants with a high-germination-rate strategy are common in the habitat where seed mortality is high.

Figure 2. Bifurcation diagram as a function of the dispersal rate D . Black circles, ESS; white circles, evolutionary branching point. Black squares (G_1^*) and black triangles (G_2^*) indicate the germination strategies in the evolutionarily stable coalition. The white square and triangle at $D = 0$ indicate the within-habitat ESSs with no dispersal in habitat 1 and habitat 2, respectively. Parameters: $s_1 = 0.9$, $s_2 = 0.1$, $p = 0.7$, $k = 10^4$, $a = 4$.

3. BIFURCATION ANALYSIS

The amount of seeds exchanged via dispersal between the habitats is critical for the development of polymorphism. The bifurcation diagram in figure 2 shows that in order to get evolutionary branching, the dispersal rate between the habitats must be small. In case of high-dispersal, the strategies experience both habitats frequently. A common generalist strategy outcompetes all other strategies that are uniquely adapted to just one of the individual habitats and this leads to the evolution of a single generalist ESS germination fraction.

Our simulations indicate that as the dispersal rate decreases, an evolutionarily stable coalition of high- and low-germination strategies appears but the monomorphic population of a generalist strategy is still a local ESS. In this case, the evolutionarily stable coalition cannot be attained from a monomorphic population by evolutionary branching. However, if the population becomes dimorphic by an occasional mutation of large effect or by immigration, then it may converge to the evolutionarily stable coalition. When the dispersal rate decreases further, the ESS bifurcates into an evolutionarily branching point. At this point the monomorphic population undergoes evolutionary branching and evolves to the evolutionarily stable coalition of high- and low-germination strategies. The bifurcation pattern in figure 2 is a robust pattern of adaptive dynamics and can be derived from its basic principles (appendix in Geritz *et al.* 1999).

Strategies in an evolutionarily stable coalition are different from the ESSs of independent habitats with no dispersal, because even if only a small fraction of individuals disperses, it is still worthwhile being slightly adapted to the environment of the other habitat. However, as the dispersal rate approaches zero, the coexisting strategies become gradually similar to the single-habitat ESSs. Note that a low level of dispersal between the habitats does not mean two evolutionarily independent populations: in the absence of one strategy, the other strategy undergoes swift evolution towards the branching point where the population becomes dimorphic again.

The two strategies of the evolutionarily stable coalition are adapted to the different ecological properties (seed

Figure 3. Shaded areas indicate the combinations of mortality rates ($1 - s_1$) and ($1 - s_2$) for which evolutionary branching occurs. (a) Change of parameter region with respect to the probability of good years p , when the dispersal rate is fixed at $D = 0.02$. Shaded areas: dark, $p = 0.4$; grey, $p = 0.6$; light grey, $p = 0.8$. (b) Change of parameter region with respect to the dispersal rate D , with fixed probability of good years $p = 0.6$. Shaded areas: dark, $D = 0.04$; grey, $D = 0.03$; light grey, $D = 0.02$.

survival) of the two habitats. In figure 3 the shaded areas represent the range of the $1 - s_1$ and $1 - s_2$ mortality rates where the germination rate undergoes evolutionary branching, i.e. where germination dimorphism develops inevitably. When the probability of good years is higher or the dispersal rate between the habitats is lower, then the parameter region of mortality rates leading to evolutionary branching is wider. This suggests that high-quality environments with a high probability of good years foster the coexistence of different strategies and also emphasizes the importance of restricted dispersal between habitats in the maintenance of polymorphism.

4. DISCUSSION

We have shown that two strategies with different germination fractions can coexist and form an evolutionarily stable coalition when the mortality rates of seeds in the soil differ between habitats. Restricted dispersal is needed for evolutionary branching of germination strategies, and the distribution of above-ground environmental fluctuations also has a significant effect on the development of polymorphisms. Assuming only two different habitats, evolution attained a stable coalition of two strategies. This may suggest that in increasing the number of different habitats, the level of polymorphisms also increases. In an environment consisting of three habitats we found that the evolutionarily stable coexistence of three distinct germination strategies is indeed possible.

It is only the combined effect of temporal fluctuations, spatial heterogeneity and density dependence that leads to evolutionary branching and evolutionarily stable coalitions of germination fractions. In a spatially homogeneous population with no density dependence there exists a single optimal germination fraction, which can be easily found by the maximization of the long-term growth rate (Cohen 1966). Spatial heterogeneity itself does not affect the existence of a single optimal germination fraction. In a spatially heterogeneous environment the population is characterized by a vector of seed numbers in different patches and the population dynamics is described by stochastic projection matrices. There is a well-defined

long-term growth rate attached to each germination strategy to which the maximization principle can be applied (Tuljapurkar 1989). Including density dependence changes the problem significantly. The long-term growth rate of a strategy is determined by the joint distribution of the environment and the density. Since the density distribution is set by the resident's strategy, the long-term fitness of a mutant becomes frequency dependent (Kisdi & Meszéna 1993, 1995). Although in a spatially homogeneous environment there is a single global ESS germination rate under density dependence (Bulmer 1984; Ellner 1985a), spatial heterogeneity makes evolutionary branching and evolutionarily stable coalitions of germination strategies possible.

The prevalence of a single mixed strategy or the coexistence of several pure strategies are often thought of as two complementary possibilities. In matrix games the coexistence of mixed strategies is neutral as long as their mixture yields the same ESS (Thomas 1984). In fluctuating environments, however, where the long-term growth rate is a nonlinear function of the strategy itself, a monomorphic population of a mixed strategy markedly differs from a coalition of pure (or mixed) strategies (cf. Bulmer 1984). When several strategies coexist, their frequencies fluctuate as consecutive years favour different strategies over others. By contrast, in the monomorphic case, the frequencies of the different pure strategies are fixed within a single mixed strategy. As coalitions of mixed strategies are not equivalent to each other or to a single mixed strategy in fluctuating environments, the evolutionarily stable coalition is a unique evolutionary outcome that cannot be replaced by any single mixed strategy.

Evolutionarily stable polymorphisms of mixed strategies have been only found in the evolution of dispersal rate (Ludwig & Levin 1991; McPeck & Holt 1992). Recent studies indicate that polymorphism of dispersal strategies may emerge by evolutionary branching in populations with non-equilibrium dynamics (Doebeli & Ruxton 1997; Parvinen 1999) or in stochastically varying, spatially heterogeneous environments (Mathias *et al.* 2001).

Analysis of the model required the assumption of very large populations. Finite-population simulations revealed that evolutionary branching does not guarantee the persistence of a polymorphism (see Mathias & Kisdi 2002). The density of a strategy may fluctuate widely, and in finite populations, occasionally may reach zero even if the strategy has a positive long-term, low-density growth rate when rare. Extinction of one strategy is followed by evolutionary branching in repeated cycles, which results in a cyclic evolutionary tree that is reminiscent of iterative evolution.

Evolutionary branching or evolutionarily stable coalitions of pure strategies chosen from a continuous strategy set have been found in constant environment models assuming spatial heterogeneity and density dependence operating within the patches (Brown & Pavlovic 1992; Meszéna *et al.* 1997; Kisdi & Geritz 1999; Geritz & Kisdi 2000; Day 2000). In a similar way to our results, these models generally show that restricted dispersal facilitates the evolution of polymorphism (although a very small dispersal rate may lead to a single specialist ESS rather than to evolutionary branching; Meszéna *et al.* 1997; Day 2000).

Will evolution promote low rates of dispersal rate that in turn facilitate the coexistence of different germination strategies? Adaptation to local environmental conditions selects against dispersal (Asmussen 1983; Kisdi 2002). Since each germination strategy is better adapted to one of the habitats, we might expect that dispersal will decrease in populations that are polymorphic for the germination rate. However, dispersal is advantageous in stochastic environments, for spreading the risk of environmental fluctuations and for escaping from local crowding. Generally, in multi-patch habitats non-synchronized temporal variability selects for dispersal (Levin *et al.* 1984; Cohen & Levin 1991). In our model the fluctuations are synchronized over the habitats, hence the environmental fluctuations themselves cannot select for higher dispersal rates. Escape from crowding nevertheless makes dispersal advantageous, and by simulating dispersal evolution, we found that the dispersal rate increased provided that no direct cost was entailed. The benefits of dispersal however, often come at a cost of, for example, increased mortality during dispersal or decreased fecundity due to investment in dispersal-related traits. With high cost of dispersal we found that the dispersal rate decreased during evolution. Selection for decreased dispersal is stronger in the low-germination strategy, which confirms the predictions of a selective trade-off between dormancy and dispersal (e.g. Klinkhamer *et al.* 1987; Venable & Brown 1988).

Since different germination strategies are associated with different habitats, restricted dispersal between habitats provides partial reproductive isolation. Other seed traits such as seed size are often strongly related to germination rate. These traits, in turn, may influence the optimal timing of reproduction, whereby different strategies may cease to interbreed. Disruptive selection during evolutionary branching itself facilitates reproductive isolation (Dieckmann & Doebeli 1999; Geritz & Kisdi 2000). The evolutionary branching of germination strategies therefore may eventually lead to parapatric speciation.

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