Disturbance-generated niche-segregation in a structured metapopulation model

Kalle Parvinen

Department of Mathematics, FIN-20014 University of Turku, Finland

`kalparvi@utu.fi`

and

Géza Meszéna

Department of Biological Physics, Eötvös University, Pázmány 1A, Budapest, H-1117
Hungary

`geza.meszena@elte.hu`

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ABSTRACT

In studying coexistence that is maintained by local disturbances via a trade-off between fecundity and competitivity, we use the theory of structured metapopulations to consider the local- and metapopulation-scale dynamics on the same footing. In contrast to the predictions of the usual patch-occupancy models, our study reveals that this kind of diversity, while certainly possible, is severely constrained by the requirement of partitioning of the continuum of patches with different population densities, i.e., patches of different ages. Adaptive dynamics, evolutionary stable coalitions and evolutionary branching are investigated in the model. We conclude that the partitioning of the patch-age, as a niche dimension, does not differ in any essential respect from partitioning of a resource-axis.

Subject headings: Diversity, disturbance, niche, metapopulation

1. Introduction

Maintenance of species diversity via disturbance (Connell 1978; Hastings 1980; Huston 1979, 1994) is a central issue of ecology. In the most commonly considered case, it is assumed that the ability to colonize and/or exploit an empty habitat can be increased at the cost of decreasing local competitiveness. In a constant environment, the better competitors (the "K-strategists") outcompete the good colonizers/exploiters (the "r-strategists") in each habitat, so the latter ones disappear. If, however, the local sub-populations are destroyed regularly, the r-strategists may always have a chance to exploit a newly emptied habitat before they are expelled from the previous one. This way, the long-term coexistence of the r- and K-strategist (or "early-successional" and "late successional" species, Rees et al. 2001) is maintained.

Such mechanism requires a metapopulation (Levins 1968) structure, i.e., a collection of local populations connected via dispersal. The usual way of modelling is based on a serious simplification: a patch is either empty, or fully occupied by a single species (e.g. Nee and May 1992; Amarasekare et al. 2004). Occupied patches become empty due to catastrophes. Empty patches become occupied, when colonized by dispersers from the occupied patches. In this context, better competitive ability is modelled via the possibility of overcolonization of the less competitive species. These "patch occupancy" models can also be interpreted outside the patch disturbance framework, as one can define the "patch" as a single "safe site", possibly occupied by a single individual (Tilman et al. 1994; Calcagno et al. 2006; Geritz 1995; Geritz et al. 1999; Kisdi and Geritz 2003).

As we are interested in disturbance-mediated coexistence, we stick to the original "population of populations" interpretation of metapopulation modelling. In this context, overcolonization is a process in which the more competitive species gradually ousts the other one from the patch. This succession may take many generations. As the traditional metapopulation models do not follow the local population dynamics, the details of the real process of colonization and competition remain hidden. Here we look for a deeper understanding via following the population growth and the process of competitive exclusion within the patches explicitly, i.e., by considering the local- and metapopulation-scale dynamics on the same footing. To this end, we study the phenomenon in a *structured* metapopulation model (Gyllenberg and Metz 2001; Metz and Gyllenberg 2001; Parvinen and Egas 2004; Parvinen 2006).

There are two basic ways of being an r-strategist (Pacala and Rees 1998). Either, it can be a good colonizer that arrives first to the empty patch. This is the widely investigated case of competition-colonization trade-off (Hastings 1980; Nee and May 1992; Tilman et al. 1994; Calcagno et al. 2006; Kinzig et al. 1999). Or, the r-strategist can exploit the resource-rich environment of the new habitat faster, than the K-strategists (successional niche segregation, Pacala and Rees 1998; Szabó and Meszéna 2007). The latter type of trade-off is our choice for the current investigation.

2. Model definition

We adapt our model from the structured metapopulation model of Parvinen (2006) by introducing the trade-off, that decreased fecundity is the cost of increased within-patch, or local, competitivity. The dispersal properties are the same for all variants. An infinite number of habitat patches is assumed. For numerical simplicity, discrete, non-overlapping generations are used. Individuals reproduce once and die afterwards; simulation steps follow the generations. In each step, after reproduction, a fraction d of the newborns enters the dispersal pool; the rest remains in their original patch. Dispersers survive to the next step with probability k and immigrate into a randomly chosen patch with probability α. In any patch, the immigrants and the non-dispersed individuals together form the parent population for the next reproduction. Catastrophes may occur randomly in any patch after the dispersal process. The probability μ of a catastrophe is independent of the local population size. A catastrophe kills all individuals in the patch. Nevertheless, the patch remains habitable, and can be re-colonized by dispersers from the disperser pool.

The fecundity $f\left(s, \sum N\right)$ of an individual depends on its inherited “strategy” s that characterizes the species, and on the total density $\sum N$ of the individuals in the patch. The latter dependence is of the Ricker-type (Ricker 1954)

$$f\left(s, \sum N\right) = f_0(s) \exp\left(-\frac{\sum N}{K(s)} \ln f_0(s)\right),$$

where $f_0(s) = f(s,0)$ is the fecundity at zero density. The carrying capacity $K(s)$ is the equilibrium density, when the strategy is alone in an isolated patch. (That is, $f(s, K(s)) = 1$ for all s.) It can be considered as the measure of the local competitivity: In absence of catastrophes, species with the largest K outcompetes all others from all patches.

The strategy $s \in [0, 1)$ characterizes the species along the r-K continuum. We assume the dependences $K(s) = (1 - s)^{1/\beta}$ and $f_0(s) = 1 + \gamma s^{1/\beta}$. The value $s = 0$ corresponds to the extreme K strategy that maximizes the carrying capacity; $K(0)$ is scaled to 1. When s approaches 1, fecundity increases, while the carrying capacity goes to zero. This end of the scale represents the r strategy. Parameter β scales the shape of the trade-off (Fig. 1). It is concave for $0 < \beta < 1$ and convex for $\beta > 1$. Parameter γ determines the maximal possible value of fecundity.

3. Results

Fig. 2 illustrates coexistence of four different species. In the left panel their abundances $N_s(t)$ in a single patch are plotted as a function of the patch age t since the last catastrophe.

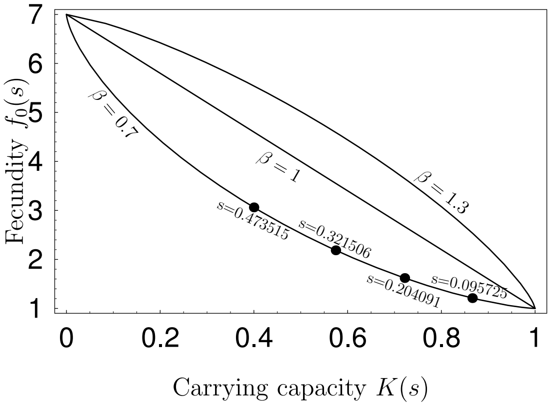

Fig. 1.— Trade-off between fecundity $f_0(s)$ and local carrying capacity $K(s)$ for the parameter values $\beta = 0.7$ (concave trade-off), $\beta = 1$ (linear), and $\beta = 1.3$ (convex); $\gamma = 6$. The four dots on the concave curve represent the four strategies in Fig. 2.

With the given parameters, the local population dynamical processes are much longer than the generation time, so we have reasonably smooth time-courses. The probability that a patch survives until a given age is plotted as a thick curve. On the right panel one can observe that, initially, the species with the largest colonization ability has the highest fecundity. It loses its advantage and is taken over by another species with lower colonization, but higher competitive ability, when the total size of the local population increases and the local competition increases. This pattern of succession is repeated until the species with the largest competitive ability reaches its carrying capacity.

How many strategies can actually coexist in the metapopulation? In particular, would it be possible to invade the established coalition by a new species? To tackle these issues we need a notion of fitness. In general, fitness is the long-term exponential growth rate of an invader in an environment set by the resident coalition (Metz et al. 1992). A newly arrived strategy invades if, and only if, its fitness is positive. The fitness is zero for an equilibrium population. In the metapopulation setting we find it more convenient to study fitness as the logarithm of the basic reproduction ratio R_m of the *dispersal* generations. R_m is defined

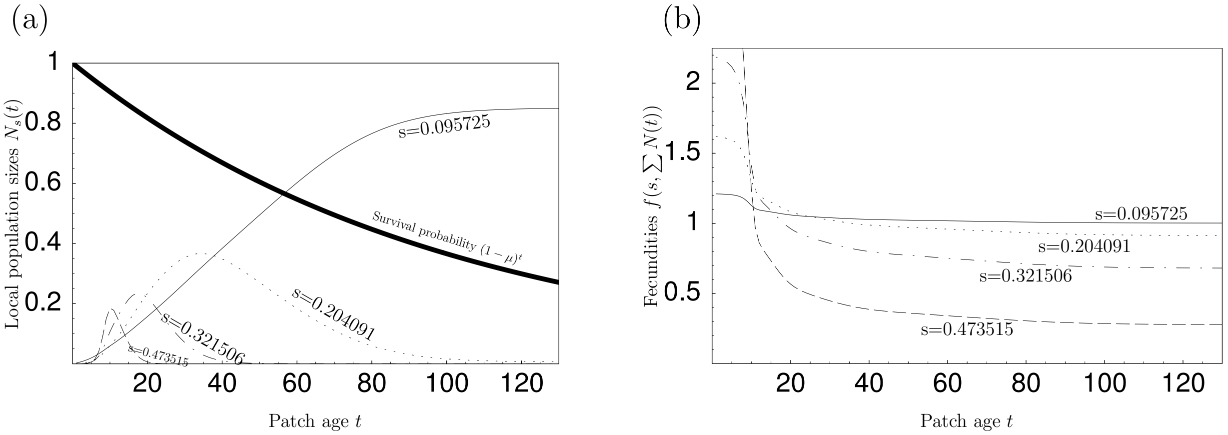

Fig. 2.— Coexistence of four different strategies. Local population size (a) and fecundity (b) of the strategies as a function of patch age. The thick curve on panel (a) represents the survival probability of the patch until the specified age. Note that the strategy with the highest K dominates the old patches. However, only a fraction of the patches survives so long. (Parameters: $\beta = 0.7$, $\gamma = 6$, $d = 0.005$, $k = 0.95$, $\alpha = 0.8$, $\mu = 0.01$. The same values are used in the other figures when not specified otherwise.

as the expected number of dispersers produced by the clan initiated by a mutant disperser in the environment set by the resident (Gyllenberg and Metz 2001; Metz and Gyllenberg 2001; Parvinen 2006). (Do not confuse dispersal generation with the individual generation. The former one constitutes a variable number of the latter one.) The (sign) equivalence of the two fitness measures is a non-trivial result (Gyllenberg and Metz 2001; Metz and Gyllenberg 2001).

Fig. 3a presents the fitness function when the coalition of Fig. 2 is established. The four established strategies have zero fitness, as expected. The non-trivial feature is that all other strategies have negative fitness. It means that the four strategies chosen for Fig. 2 form an uninvadable, i.e., an evolutionarily stable coalition.

How does one reach such an uninvadable strategy coalition? One option is to assume that all strategies (with a discretization) are present initially. Then one can follow the metapopulation dynamics and see which strategies remain, as illustrated in Fig. 3b. (Here we iterated the dispersal generations using the calculated R_m values for each strategy. As the dispersal generations are of unequal length, this simulation does not exactly match the real time-course. Nevertheless, the final state is unaffected.) We observe that the strategies very soon form several clusters. The width of these clusters becomes narrower in time. Except of the effect of the discretization, the end result is the uninvadable coalition of Fig. 2.

Fig. 3c represents the possibility of evolutionary emergence of an uninvadable coalition starting from a single strategy. Here we iterated the real local population dynamics (reproduction and dispersal) and random catastrophes in 1000 patches. Every 1000^{th} generation was considered as a single evolutionary step. In each of these steps a single random mutation occurs. (A strategy slightly different from a randomly chosen present strategy is introduced with a small population size. Mutation step size follows a Gaussian distribution with standard deviation 0.01.) Repeated mutations and invasions result in the change of the strategies constituting the coalition. One can observe several consecutive events of evolutionary branching (Geritz et al. 1997, 1998). The evolutionary process ends up in the same uninvadable coalition again, now with a cloud of mutants. Note, however, that the uninvadable coalitions obtained with the two described methods are not necessarily always equal.

Fig. 4 depicts the parameter-dependence of the final coalition obtained starting from all strategies (with a discretization). We observe that coexistence of four strategies is common; coexistence of five ones is restricted to narrow parameter ranges. The β dependence shows that, given the other parameters, the investigated trade-off curve with $\beta = 0.7$ is around to be optimal to maintain diversity. If the disturbance rate is high, i.e., the average patch lifetime $\frac{1}{\mu}$ is short, only the extreme r strategist survives. Longer patch ages allow coexistence such, that the average strategy of all individuals moves to the direction of K strategy. At low disturbance rate the most competitive species becomes dominant, as one can observe from the change of the average strategy.

Evolutionarily stable coalition of more than five strategies was not observed. As we are not aware of, or hope for, an analytic way of proving an upper bound of the number of coexisting strategies, we cannot exclude the possibility of model versions supporting a slightly larger coalition. Nevertheless, the limited possibility maintaining high diversity this way is a clear conclusion.

4. Discussion

Understanding the factors shaping species diversity is a fundamental problem with great practical relevance for nature conservation. The role of environmental fluctuations is an important focus of investigation. Here we analysed the possibility of coexistence maintained by a trade-off between fecundity and local competitivity via a structured metapopulation model. The novelty of our approach is that we follow the local as well as the metapopulation-scale dynamics. This way we acquired a clearer picture on the possibility of disturbance-related coexistence than the one was provided by the patch-occupancy models. We found that coexistence is based on, and constrained by, the possibility of the successional segregation along the patch-age axis. Evolutionary stability of the coexisting coalition was analysed.

Applicability of limiting similarity (MacArthur and Levins 1967; Abrams 1983) was noted already in the patch occupancy models. However, one is free to choose the parameters describing overcolonization in that framework. Therefore, coexistence of an arbitrary number of species can be arranged (Tilman et al. 1994). Augmentation of the picture with the possibility of back-colonization results in further constraining the coexistence of similars (Kinzig et al. 1999). Still, with proper choice of the parameters, one can arrange arbitrarily large coalitions. This behavior is in line with the fact that the patch occupancy models are isomorphic to the asymmetric version of the Lotka-Volterra competition model (Kisdi 1999). Existence, or non-existence of back-colonization corresponds to the non-extreme, or extreme asymmetry of competition, respectively (see Geritz 1995; Geritz et al. 1999 for this distinction within non-Lotka-Volterra site occupancy models).

When mechanistic details of the local replacement process are factored in, as in the current investigation, the possibilities are more constrained. The expected patch life-time should be long enough to allow several successional steps that cannot be speeded up arbitrarily. However, longevity of the patches is detrimental for the r-strategists: The lower rate of disturbances decreases the ratio of the fresh patches needed for them. Therefore, in agreement with the intermediate disturbance hypothesis (Connell 1978), neither the low, nor the high level of disturbance supports significant diversity. In between, for intermediate levels of the catastrophe rate, coexistence of several, but not very many, successional states were observed.

It is also possible to model the successional replacement process within a single patch (e.g. Fig. 6.1 in Tilman 1988, p. 187). However, if a single habitat of finite lifetime is considered separately, the long-term survival of the species at the metapopulation scale is defined outside the scope of the study. In this case one has to *postulate* the set of species, that has the possibility to enter the habitat. To see the complete picture, parallel consideration of the local and the global scales was essential. On the one hand, the global-scale competitive exclusion determines the species composition of the metapopulation. On the other hand, study of the local operation of successional replacement provides the constraints for the global-level processes. See Szabó and Meszéna (2007) for another study of this kind.

The presented results are consistent with the general impression about the real-word processes. In particular, our Fig. 2 is very reminiscent to the empirically observed succession (Fig. 8.22 of Tilman 1988, p. 284).

Our investigation is inherently related to a major debate of community ecology. Niche theory (Hutchinson 1978; Leibold 1995; Chase and Leibold 2003), a centrepiece of classical ecology, asserts that competitive exclusion operates between species attempting to occupy the same niche, so the availability of the different niches constraints diversity. In contrast, the theory of disturbances (Connell 1978; Hastings 1980; Huston 1979, 1994) argues that repeated disturbances in a non-equilibrium ecosystem are able to increase diversity beyond the prediction of the equilibrium theory via weakening competition.

The controversy about, and the axiomatic status of, the competitive exclusion principle (”complete competitors cannot coexist”) was reviewed already in the seminal paper of Hardin (1960). While the principle played a key role in Hutchinson’s concept of niche (Hutchinson 1978), he also introduced the doubt that the non-equilibrium situations may be entirely different (“paradox of the plankton”, Hutchinson 1961). These distinctions between equilibrium and non-equilibrium, niche and disturbance are used to be regarded as fundamental (Huston 1979, 1994).

However, Hardin’s argument about the unavoidability of niche segregation was reformulated for fluctuating situations by Chesson (1991). A general theory of fluctuation-mediated coexistence was developed on this basis (Chesson 1994, 2000a,b). The fallacy of the idea, that ”disturbance” decreases ”competition” somehow in a general way, was discussed in detail by Chesson and Huntly (1997). In line with the emergence of this new synthesis, the disturbance-maintained coexistence is now also considered as a niche-segregation along life-history trade-offs (Rees et al. 2001; Amarasekare 2003).

Our model is a clear demonstration of the non-existence of a principal difference between equilibrium and non-equilibrium ecology. We considered the very ecological situation which is the archetype of the fluctuation-maintained diversity. Nevertheless, the same pattern can also be seen as an equilibrium one. At the metapopulation level, the dynamical variables of the model are the $N_s(t)$ distribution functions. For each strategy, it specifies the distribution of the population between the patches of different ages. In terms of these variables, the dynamics is deterministic and converges to the equilibrium distribution displayed in Fig. 2.

From the local point of view, the less competitive r-strategist species are able to survive temporarily because catastrophes transitionally reduce local competition. However, the global situation cannot be described as if "competition", in general, would be weaker than in equilibrium. It is neither justified to regard the r-strategist as a weak competitor on the metapopulation scale. As both kinds of simulations (Figs. 2b and 2cd) demonstrate, the metapopulation-level competition is reduced only between sufficiently different strategies that present in different periods during the succession process. Competition remains strong against the intermediate strategies. This is exactly the picture of niche-segregation: Coexistence is made possible by the reduced between-species competition. In turn, weakening of competition is caused by adaptations to different ecological roles. In our case, these roles are the presence of the species at the different successional stages. That is, the essential issue is the partitioning of the patch age, as a niche dimension. An r-strategist species, if survives, is the best competitor in its own niche.

A general theory of niche-segregation, formulated for equilibrium, was proposed elsewhere (Meszéna et al. 2006, see also Gyllenberg and Meszéna 2005). It is based on the notion of the "regulating variables", i.e., on the environmental variables involved in the feedback loop of population regulation, like resource concentrations. The theory states that coexisting species should differ in their relation to these variables. More specifically: they should differ both on their (differential) impact on, and sensitivity towards, the regulating variables. Similarity in these respects restricts coexistence to a narrow range of the parameters, i.e., makes it unlikely.

Accordingly, the set of regulating variables constitutes the niche space to be partitioned between the species (Meszéna et al. 2006). In case of a resource continuum (e.g., a continuum of food size), this set is a continuous one: the resource concentrations for all food-sizes have to be considered as separate regulating variables. Then the theory reduces to the well-known picture of resource partitioning. While there is no absolute lower bound of similarity for the coexisting populations, as a rule of thumb, the usual idea of niche segregation prevails (Szabó and Meszéna 2006; Barabás and Meszéna, *in prep.*).

This equilibrium theory applies to our model without any caveat. Here the total density $\sum N(t)$ for the patch-age t plays the role of regulating variable. It describes the resource exploitation, i.e. the strength of competition in the patches of age t. If this quantity is known for all patch-ages, then the fecundities of the different strategies in any patch are calculable. This way, we have a continuum of the regulating variables along the patch-age axis. It is in a complete analogy with the continuum of resource densities (more exactly: the exploitations thereof) in the food-size case.

In this study we opted to keep the dispersion parameters constant. In reality, one can expect the dispersion rate to be optimized at a higher value for an r-strategist, than for a K-strategist. Moreover, the higher migration rate itself (even without higher fecundity, as in the pure case of competition-colonization trade-off, cf. Pacala and Rees 1998) can contribute to the r-strategist nature of a species. In general, one should consider a trade-off between three variables: fecundity, dispersal and competitivity. However, the mathematical structure would remain similar to our one. If the populations within a single patch are regulated by a single factor, then the whole metapopulation is regulated by the patch-age continuum of this factor. Coexistence in such a system is an issue of niche-segregation along the patch-age axis.

The issue of the optimal value of dispersion parameters is related to the evolutionary origin of the r strategy. Tilman (1988) considers fast vegetative growth, which may, or may not be coupled to fast reproduction, as an adaptation to high rate of biomass loss e.g. by herbivory. Such r strategists need not have a high dispersion rate, and will not has it because of the trade-off between migration ability and the other life-history parameters. Still, they will dominate the early stages of succession if they happen to find their way to the place. In contrast, if the early stages of the succession in a metapopulation with repeated patch catastrophes is the typical niche of an r strategist, then it is necessarily selected for higher migration rate.

Note, that the term “disturbance” is not always defined with clear distinction between a constantly high loss rate and repeated patch catastrophes. While both situations select for high growth rate, only the second one is able to maintain diversity by providing a new opportunity for niche segregation. A constant high rate of biomass loss does not introduce any new regulating variable. This is, again, in line with the conclusion of Chesson and Huntly (1997) that “harshness” of the environment, alone, neither decreases competition, nor increases diversity.

In our model, the abiotic environment remains constant between the catastrophes. It is like a secondary succession, when fertile soil is available from the very beginning. In case of primary succession, one should take into account the facilitating effects of the populations. Then, an additional variable (e.g. soil nitrogen level, cf. Tilman 1988, p. 214) should be followed as a function of the patch age. Still, age remains a full characterization of a patch. Therefore, the picture of niche-segregation along the patch-age axis would survive. If the "resource ratio hypothesis" of the primary succession (Tilman 1988, p. 217) is to be modelled explicitly, then one should consider two local regulating variables (e.g. soil nitrogen level and light intensity on the soil surface) instead of a single one, like the total density used here. Then, at the metapopulation level, the set of regulating variables consists of the two patch-age-continuums of the two local regulating variables. All of such details are completely overlooked by the patch occupancy models.

The *complete* extinction at patch catastrophe was an essential ingredient of our model. This assumption ensures that patch-age (i.e., the time spent since the last catastrophe in the patch) is a full descriptor of the state of the patch. The possibility of partial catastrophes would require considering the whole history of disturbances at any localities. Niche analysis of such situation is beyond our scope here.

It is an ongoing controversy whether evolutionary branching, that occurs in non-genetic models, can be interpreted as a minimal representation of (the ecological aspects of) speciation (see Dieckmann et al. 2004; Gavrilets 2005 for the opposing views; Dieckmann and Doebeli 1999; Pennings et al. 2008 for model studies). Note also that species coexisting along the r-K continuum are often not closely related to each other. Therefore, their evolution cannot be described solely in our context. Still, the observed branching pattern demonstrates in principle, that the relation between ecology and evolution is the same for the disturbance-maintained and for the resource-competition-maintained diversity. In both cases, the niche-theoretic "decreasing competition with increasing difference" translates to the possibility of disruptive selection and evolutionary branching (cf. Christiansen 1988 for the case of resource competition). The Darwinian picture (Darwin 1859, p. 76), that competition between the similar kinds drives evolution, while the decreased competition between the differing species allows them to coexist, prevails. In contrast, the status of natural selection would be unclear under a kind of general weakening of competition by disturbance. This way, evolutionary considerations reinforce the deep connection between disturbance and niche.

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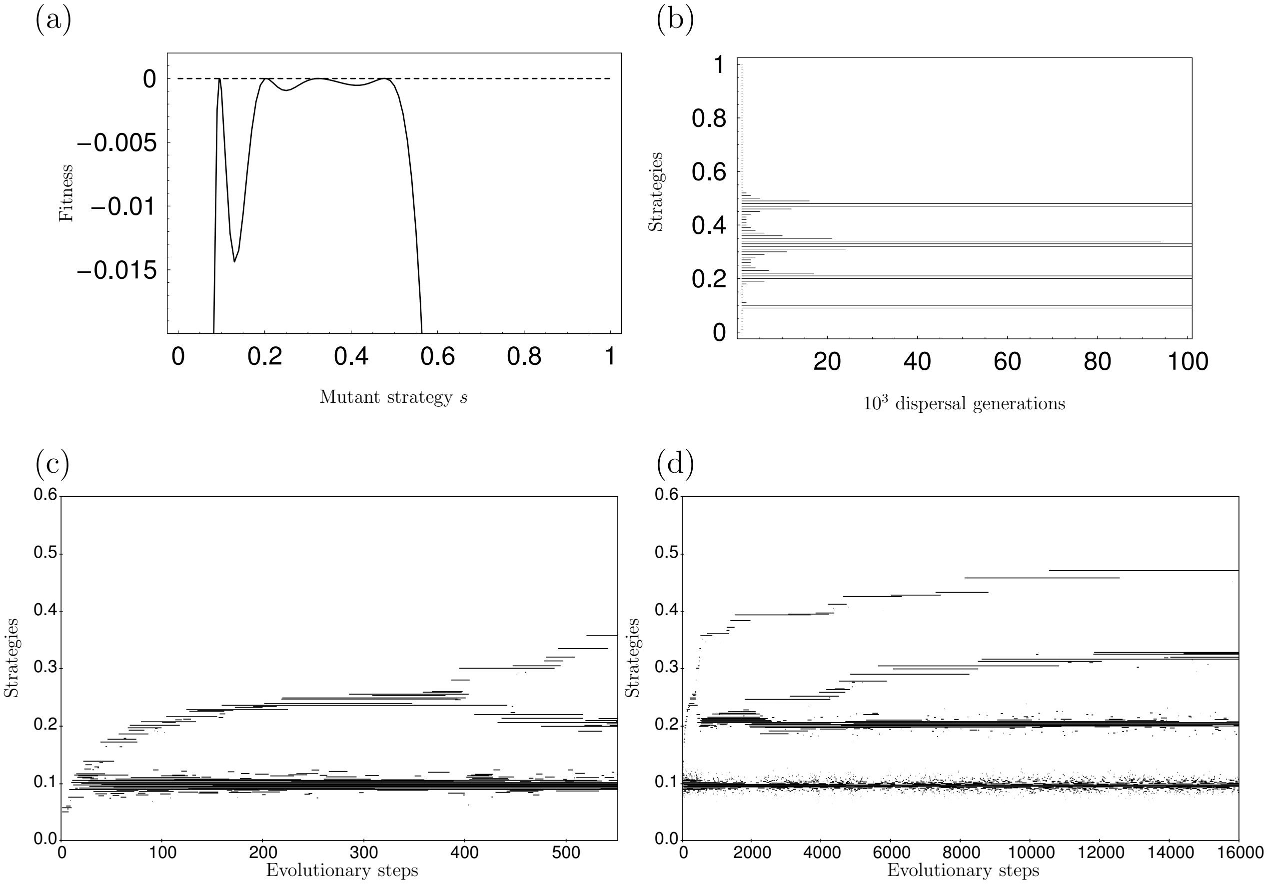

Fig. 3.— Evolutionary considerations. (a) Fitness as a function of the strategy provided, that the coalition of Fig. 2 is present in the metapopulation-level equilibrium. Observe that the four strategies forming the coalition are local fitness maxima; the maximum is equal to zero by the equilibrium condition. All other strategies have negative fitness, so the coalition is an evolutionary stable one. (b) Simulation initiated with 101 strategies 0, 0.01, 0.02,. . ., 0.99, 1. Most of the strategies die out soon. The surviving coalition is essentially the same, as was presented in Fig. 2. Evolutionary simulation with mutation (c and d) starting from a single strategy plotted on two different time scales. Again, essentially the same coalition emerges.

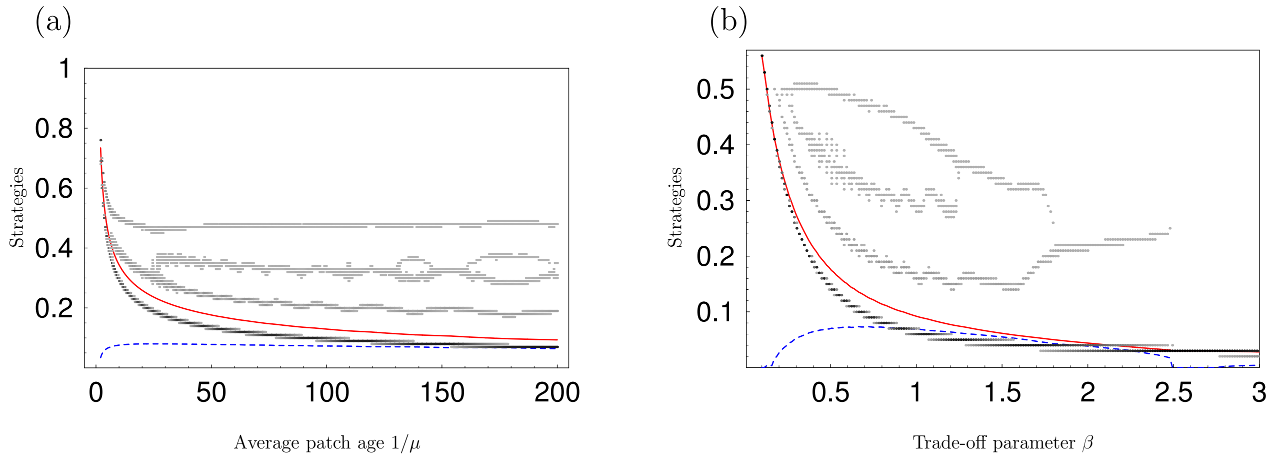

Fig. 4.— Parameter dependence of the surviving coalition in a simulation initiated like in Fig. 3b. Darkness represents abundance in the coalition. (a) Dependence on average patch age $1/\mu$. (b) Dependence on the trade-off parameter β. The average overall strategy is plotted with a thin solid curve, and the standard deviation of the strategy distribution with a dotted curve.

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