

Adaptive diversity in heterogeneous environments for populations regulated by a mixture of soft and hard selection

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ABSTRACT

The stable co-existence of two haploid genotypes or two species is studied in a spatially heterogeneous environment submitted to a mixture of soft selection (within-patch regulation) and hard selection (outside-patch regulation) and where two kinds of resource are available. This is analysed both at an ecological time-scale (short term) and at an evolutionary time-scale (long term). At an ecological scale, we show that co-existence is very unlikely if the two competitors are symmetrical specialists exploiting different resources. In this case, the most favourable conditions are met when the two resources are equally available, a situation that should favour generalists at an evolutionary scale. Alternatively, low within-patch density dependence (soft selection) enhances the co-existence between two slightly different specialists of the most available resource. This results from the opposing forces that are acting in hard and soft regulation modes. In the case of unbalanced accessibility to the two resources, hard selection favours the most specialized genotype, whereas soft selection strongly favours the less specialized one. Our results suggest that competition for different resources may be difficult to demonstrate in the wild even when it is a key factor in the maintenance of adaptive diversity. At an evolutionary scale, a monomorphic invasive evolutionarily stable strategy (ESS) always exists. When a linear trade-off exists between survival in one habitat versus that in another, this ESS lies between an absolute adjustment of survival to niche size (for mainly soft-regulated populations) and absolute survival (specialization) in a single niche (for mainly hard-regulated populations). This suggests that environments in agreement with the assumptions of such models should lead to an absence of adaptive variation in the long term.

Keywords: adaptive polymorphism, co-existence, density dependence, hard selection, heterogeneous environments, invasive ESS, population regulation, soft selection.

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INTRODUCTION

Over the last 40 years, there has been extensive discussion about the maintenance of multi-niche polymorphism (Levene, 1953; Dempster, 1955; Maynard-Smith, 1962, 1966, 1970; Strobeck, 1974, 1979; Gliddon and Strobeck, 1975; Gillespie, 1976; Maynard-Smith and Hoekstra, 1980; Hoekstra *et al.*, 1985; Hedrick, 1990a,b; de Meeûs *et al.*, 1993). These theoretical developments have shown that, without overdominance, polymorphism can only be maintained in soft-regulated populations (soft selection = within-patch density dependence) and never in hard-regulated ones (hard selection = outside-patch density dependence) (Maynard-Smith and Hoekstra, 1980; de Meeûs *et al.*, 1993). However, for soft-regulated populations, maintenance of polymorphism requires either a large selective differential or a nice adjustment of fitness to the niche sizes (e.g. Maynard-Smith, 1966; Maynard-Smith and Hoekstra, 1980; but see Gillespie, 1976). More realistic situations, intermediate between soft and hard selection, have attracted little attention. Maynard-Smith and Hoekstra (1980) explored a demographic model that contains hard and soft regulation as the limiting case. However, they did not derive intermediate situations between low and high density dependence within the niches. Hedrick (1990b) developed a model where population regulation followed a mixture of soft and hard selection with proportions x and $1 - x$ respectively. He did so for the classic fitness framework (i.e. perfect symmetry between the two alleles analysed) with habitat preference and reported results intermediate between those of pure soft-regulated and pure hard-regulated populations. If one assumes that mutation cannot drive its bearer far from the initial state, the symmetric fitness framework is only relevant for entities that are already reasonably divergent. Indeed, in the symmetric case, Hoekstra *et al.* (1985) showed that similar genotypes can only co-exist in a narrow range of environmental conditions (strongly disruptive selective pressures). In addition, all the studies cited above explored the conditions for adaptive polymorphism at an ecological scale (i.e. short term). At an evolutionary scale (i.e. long term), the conditions for a sustainable polymorphism are likely to be altered because the selection of new mutants or new migrants can lead the population to experience a greater variety of competitor pairs. In this paper, we investigate situations intermediate between the two extreme cases of hard and soft regulation, for different fitness functions from perfect symmetry to close identity between the two genotypes studied, both at an ecological and an evolutionary scale. At an ecological scale, when regulation is intermediate between soft and hard selection, the conditions for maintenance of polymorphism are unexpectedly broader than in soft-regulated environments, under a large array of conditions. Nevertheless, at an evolutionary time-scale, when the best genotype (invasive ESS) is sought in soft-, hard- and mixed-regulated populations, we find that populations evolving in an environment with stable ecological factors through time will always reach a monomorphic state (invasive ESS).

The basic models

We assume a Levene-type (Levene, 1953) heterogeneous environment with two resources 1 and 2 exploited by a haploid population of A and a individuals with non-overlapping generations. In this case, haploids are known to behave in the same way as diploids with complete dominance (Gliddon and Strobeck, 1975). Habitats 1 and 2 occur at rates c and $(1 - c)$ in the environment respectively. The frequency of alleles (or species) A and a is p and $q = (1 - p)$ respectively, and the fitness of an allele G in habitat i will be noted $w_i(G)$.

In each generation, propagules disperse and randomly fall into one of the two habitats, with probabilities c and $1 - c$. After settlement, viability selection occurs, followed by the production of the next generation's propagules, which again disperse. This life-cycle corresponds to many parasites (parasitic copepods: Kabata, 1981; Raibaut, 1985; de Meeûs *et al.*, 1990), marine species (polychaetes: Doyle, 1975; bivalves: Bayne, 1976; ascidians: Stoner, 1994) or species producing a large number of highly dispersible propagules (procaryotes, fungi, plants, protozoa) (e.g. Bazzaz, 1991, for plants).

After dispersal, settlement and selection, the different within-habitat frequencies of allele A are given by:

$$p_1 = \frac{pw_1(A)}{pw_1(A) + qw_1(a)}$$

and

$$p_2 = \frac{pw_2(A)}{pw_2(A) + qw_2(a)}$$

in habitat 1 and habitat 2 respectively. The relative numbers of survivors in each habitat are:

$$\bar{W}_1 = c[pw_1(A) + qw_1(a)]$$

and

$$\bar{W}_2 = (1 - c)[pw_2(A) + qw_2(a)]$$

in habitat 1 and habitat 2 respectively.

The total population is assumed to be held at a constant size N and large enough to prevent drift. The absolute numbers of survivors in each habitat are thus $N\bar{W}_1$ and $N\bar{W}_2$ for habitats 1 and 2 respectively. \bar{W}_1 and \bar{W}_2 are necessarily below 1. There must be reproduction (be it sexual, asexual or gametic) within the habitats to prevent the population from going extinct. This reproduction is such that the number of potential new colonizers is larger than or equal to N . Regulation must occur at some stage if the population is to remain at N .

In the soft selection model, this regulation occurs during within-habitat multiplication. It is such that each habitat is constrained to contribute a constant ratio to the next generation's propagule pool, which is itself of a constant size N . It is reasonable to assume that the contribution (Cb_1 and Cb_2) of each habitat is a function of its size ($Cb_i = f(c_i)$). To prevent the introduction of another parameter, the simplest solution is to assume that habitat contribution equals habitat frequency. Thus, if c is the contribution of habitat 1, one can see that each habitat produces a constant number of propagules $N_1 = cN$ and $N_2 = (1 - c)N$ at each generation (as in the model of Levene, 1953). The population is therefore totally regulated within habitats (absolute within-habitat density dependence). Consequently, in the colonizer pool of the next generation, the frequency of allele A will be:

$$p' = cp_1 + (1 - c)p_2$$

In the hard selection model, the regulation occurs outside the habitats after the propagules have left and is such that the sum of the absolute contributions of each habitat is equal to N . It can be seen that these contributions are necessarily:

$$C_1 = \frac{\bar{W}_1}{\bar{W}_1 + \bar{W}_2} N$$

and

$$C_2 = \frac{\bar{W}_2}{\bar{W}_1 + \bar{W}_2} N$$

for habitat 1 and habitat 2 respectively. In this model, therefore, there is a total absence of within-habitat density dependence. Note, however, that density dependence does indeed occur in the external environment. In the colonizer pool of the next generation, the frequency of allele A will be:

$$p' = \frac{\bar{W}_1 p_1 + \bar{W}_2 p_2}{\bar{W}_1 + \bar{W}_2}$$

Consequently, it is apparent that viability selection and regulation occur together (and thus interact) in soft-regulated populations, whereas they are decoupled in hard-regulated populations (e.g. Karlin, 1982).

Moreover, within-habitat density dependence (soft regulation) is less favourable for habitat specialization than outside-habitat density dependence (hard regulation) (Futuyma and Moreno, 1988; de Meeûs *et al.*, 1993). In other words, specialization is more likely when competition for the resource decreases.

Specialists, generalists, best genotype, trade-off and robustness

Throughout this paper, the terms 'specialist' and 'generalist' refer exclusively to the pattern of survival rates. Moreover, a genotype will be called a 'specialist' of habitat 1 if it survives better in habitat 1 than in habitat 2. A genotype $[A]$ will be said to be more specialized than $[a]$ for habitat 1 if $[A]$ survives better than $[a]$ in habitat 1. Finally, $[a]$ will be more of a 'generalist' than $[A]$ if the survival of $[a]$ is more balanced between habitats than the survival of $[A]$; namely, if $|w_2(a) - w_1(a)| < |w_1(A) - w_2(A)|$.

If we now assume that a linear trade-off exists between survival in one versus the other habitat, we can describe the survival of each genotype in the two habitats in the following manner: $w_1(A) = w_A$, $w_1(a) = w_a$, $w_2(A) = 1 - w_A$, $w_2(a) = 1 - w_a$. Alternatively, the absence of a trade-off will mean that no constraint exists on survival parameters.

Strobeck (1974) showed that for polymorphism to be maintained it is necessary and sufficient that the frequency of each allele increases when rare (protected polymorphism). We will use this property throughout this paper.

If the population is allowed to evolve (i.e. when the confrontation between every possible pair of genotypes is explored), the genotype that cannot be invaded and invades all other genotypes (invasive ESS) can be looked for. It is such that it is always protected and all other genotypes are not protected. The differences between the protected polymorphism approach and the ESS approach can be thought of as the differences between short-term (ecological time-scale) and long-term (evolutionary time-scale) processes.

Throughout this paper, the term 'robustness' has the same meaning as in Maynard-Smith and Hoekstra (1980). The wider the range of parameters (habitat productivities, survivals) allowing polymorphism, the more robust the model.

The mixed model

We now assume that regulation partly occurs within and partly occurs outside the habitats. One simple way to build the model is to consider that the environment is subdivided into two sub-environments in proportions x and $(1 - x)$, where individuals are soft- and hard-regulated respectively, as illustrated in Fig. 1. Alternatively, we could consider that a proportion x of habitats (regardless of their type) are saturated with colonizers while the remaining $1 - x$ are not. The resulting frequency of allele A in the next generation becomes

$$p' = x[cp_1 + (1 - c)p_2] + (1 - x) \frac{\bar{W}_1 p_1 + \bar{W}_2 p_2}{\bar{W}_1 + \bar{W}_2}$$

if the meta-environment is soft-regulated (model 1), or

$$p' = \frac{x[cp_1 + (1 - c)p_2] + (1 - x)[\bar{W}_1 p_1 + \bar{W}_2 p_2]}{x + (1 - x)(\bar{W}_1 + \bar{W}_2)}$$

if the meta-environment is hard-regulated (model 2).

This process may be much more realistic than the pure soft or pure hard types of regulation. For example, in host-parasite systems, parasites are aggregated over their host populations (e.g. Crofton, 1971; Anderson and Gordon, 1982; May, 1985). Some hosts will carry many parasites (saturated hosts), while most remain weakly or non-parasitized.

RESULTS

Model 1

Ecological scale

The conditions for protected polymorphism in our model are:

A protected if:

$$x \left[c \frac{w_1(A)}{w_1(a)} + (1 - c) \frac{w_2(A)}{w_2(a)} \right] + (1 - x) \frac{cw_1(A) + (1 - c)w_2(A)}{cw_1(a) + (1 - c)w_2(a)} > 1 \quad (1)$$

a protected if:

$$x \left[c \frac{w_1(a)}{w_1(A)} + (1 - c) \frac{w_2(a)}{w_2(A)} \right] + (1 - x) \frac{cw_1(a) + (1 - c)w_2(a)}{cw_1(A) + (1 - c)w_2(A)} > 1 \quad (2)$$

For convenience, in the remainder of the paper the left-hand side of inequalities (1) and (2) will be called E_1 and E_2 respectively.

Solving for (1) and (2), we obtain the following results:

- $x = 1$: these conditions reduce to those classically found (i.e. Gliddon and Strobeck, 1975) for haploids subjected to soft selection; namely, an inverse ranking of the harmonic and the arithmetic means of within-habitat relative fitness.

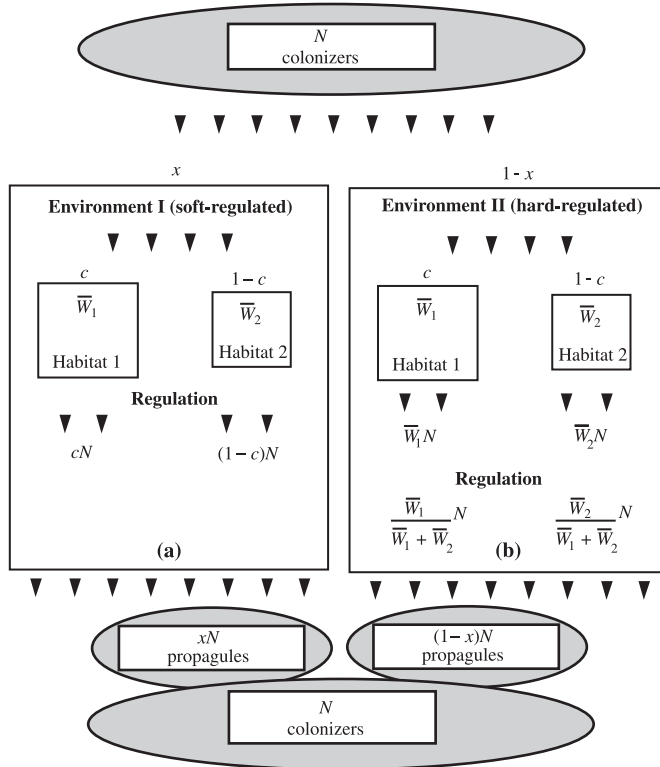


Fig. 1. Schematic representation of the mixture between Levene’s (a) and Dempster’s (b) models. The meta-environment is subdivided into two sub-environments. A random colonization of each habitat is assumed. Differential selection affects each genotype (or species) in each habitat so that the number of surviving colonizers becomes \bar{W}_1 and \bar{W}_2 . In each sub-environment, regulation occurs so that the population size is maintained at a constant size N . In Levene’s model, this regulation occurs within each habitat (i.e. coupled with selection). Thus, the contribution of each habitat remains constant in each generation (c and $(1 - c)$) and is independent of the number of surviving colonizers. In Dempster’s model, regulation occurs outside habitats, so that the contribution of each to the next generation will depend on the number of surviving colonizers found within. Then, sub-environments I and II contribute to x and $1 - x$ respectively in the colonizer pool of the next generation (model 1).

- $x = 0$: the conditions are those described by Dempster (1955) (pure hard selection model) where no polymorphism can be maintained.
- $0 < x < 1$: First we study the usual symmetrical case where A and a are equivalent specialists of habitats 1 and 2 respectively, with survival rates $w_1(A) = w_2(a) = 1$ and $w_2(A) = w_1(a) = 1 - s$ ($0 < s < 1$) (e.g. Hedrick, 1986). In this case, inequalities (1) and (2) reduce to:

$$x \left[c \frac{1}{1-s} + (1-c)(1-s) \right] + (1-x) \frac{1-(1-c)s}{1-cs} > 1$$

and

$$x \left[c(1-s) + (1-c) \frac{1}{1-s} \right] + (1-x) \frac{1-cs}{1-(1-c)s} > 1$$

Rearranging these inequalities gives the conditions on c for protected polymorphism:

$$\frac{1}{2} - \frac{\Omega - 2(1-s)}{2xs(2-s)} < c < \frac{1}{2} + \frac{\Omega - 2(1-s)}{2xs(2-s)}$$

with $\Omega = \sqrt{[xs(2-s)]^2 + 4[1-s(2-s)]}$.

Figure 2 shows that this situation accounts poorly for the maintenance of diversity and seriously lacks robustness (Maynard-Smith, 1966; Maynard-Smith and Hoekstra, 1980; Hoekstra *et al.*, 1985), unless the fitness differential s is large or c is close to 1/2. As c tends to 1/2, robustness is higher when regulation is mainly soft ($x = 1$).

However, most biological situations do not involve symmetrical habitats and fitness, and it is interesting to investigate the outcome of the competition between two similar genotypes A and a , both specialists of the same and more abundant niche (say habitat 1), with one (say a) being slightly less specialized. Assuming a linear trade-off between the two habitats:

$$w_1(A) = w_A \quad w_1(a) = w_a \quad w_2(A) = 1 - w_A \quad w_2(a) = 1 - w_a \quad (3)$$

Slight differentiation is what one might expect if one of the two genotypes arises from the other through mutation. We can then write:

$$w_1(A) = w \quad w_1(a) = (1-b)w \quad (4)$$

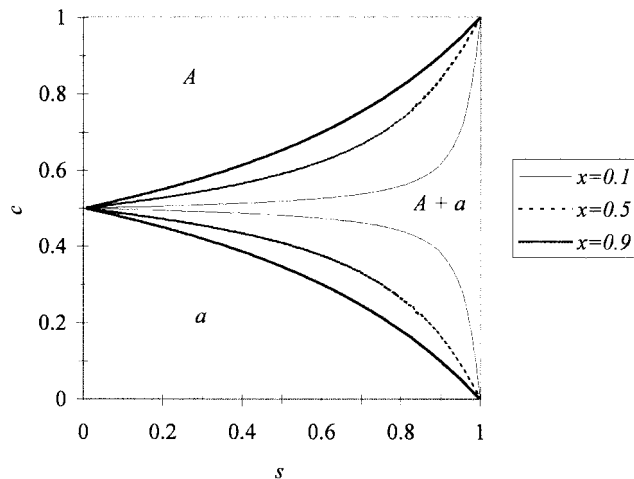


Fig. 2. Conditions for protected polymorphism when A and a are equivalent specialists of habitats 1 and 2 respectively [$w_1(A) = w_2(a) = 1$ and $w_2(A) = w_1(a) = 1-s$], for different rates of intra-niche density dependence (x). Adaptive diversity is maintained between the corresponding two curves ($A+a$). For two specialists to co-exist, either habitat productivities (c) must be balanced (close to 1/2) or selective costs (s) are high. This is more true when intra-niche density dependence (x) decreases.

Here, w represents the absolute amount of specialization of A and a on patch 1 and b reflects the effect of mutation on the loss of specialization of a relative to A . If A is the specialist of habitat 1 and if a derives from A through mutation, then b is more likely to be small (e.g. $0 < b \leq 0.1$) and $w > 0.5$. The trade-off assumption allows an analytical exploration of the model without a major loss in generalization because, in this context, the two competing genotypes are assumed to be closely related.

Solving $(E_1 - 1)(E_2 - 1) = 0$ for c , x or w gives the lower and upper parameter values (e.g. c_i and c_s respectively) between which polymorphism is maintained (similar to that shown for c in the symmetrical case). The corresponding two curves now display a strong asymmetry, making analysis of the graphics more difficult. The distance between these two values (i.e. in units of c , x or w) is a clearer representation of the robustness of the model (Maynard-Smith and Hoekstra, 1980; Hoekstra *et al.*, 1985). It shows the width between root 1 and root 2 of equations (1) and (2), between which polymorphism is maintained.

Figure 3 (Δc function of x) shows that A and a co-exist best if they are highly specialized (w large) and regulation occurs mainly, but not totally, outside the habitat (x low). A glance

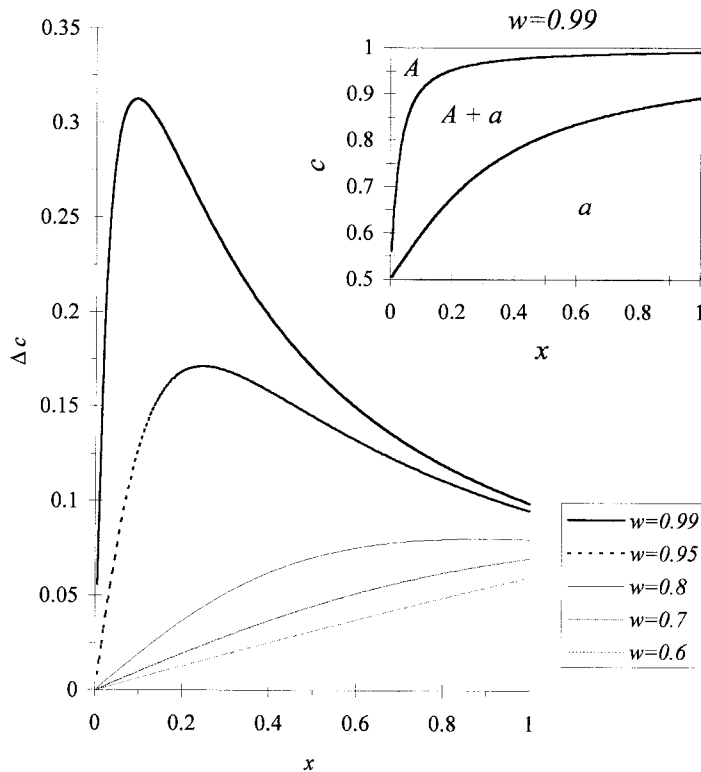


Fig. 3. The window's width ($\Delta c = c_s - c_i$) of habitat frequencies c allowing maintenance of polymorphism as a function of x for different values of w ($b = 0.1$). The little graphic in the right-hand top corner provides the details for $w = 0.99$ of the corresponding c values needed to protect polymorphism ($A + a$). Clearly, Δc is maximum for small values of x (low intra-niche density dependence). This is more pronounced in a highly specialized population (high w).

at Fig. 4 (Δx function of c) reveals that, if habitat 1 is very frequent, two specialists (high w) would co-exist under most conditions of regulation mode. With less specialization, polymorphism is better maintained with purely soft regulation and equilibrated habitat sizes ($c \approx 0.5$) (i.e. a narrow range of conditions).

Evolutionary scale

These results tell us nothing about the outcome of evolving populations. What happens if one assumes that fitness parameters can be affected by many successive mutations so that all possible genotypes can be compared? We can look for the invasive ESS in a given environment (described by x and c). This is found by solving inequalities (1) and (2) in a different way: one must always be true and the other must always be false. When no trade-off exists between survival within the different habitats, it is easy to show that the solution for the invasive ESS is a genotype \hat{A} that has a maximum survival in both habitats ($w_1(\hat{A}) = w_2(\hat{A}) = w = 1$). If a linear trade-off exists between survival in one habitat against that in the other, as previously described in (3), then a genotype A is protected when rare if:

$$c \frac{w_a}{w_A} + (1 - c) \frac{1 - w_a}{1 - w_A} > 1 \tag{5}$$

It is never invaded if:

$$c \frac{w_A}{w_a} + (1 - c) \frac{1 - w_A}{1 - w_a} \leq 1 \tag{6}$$

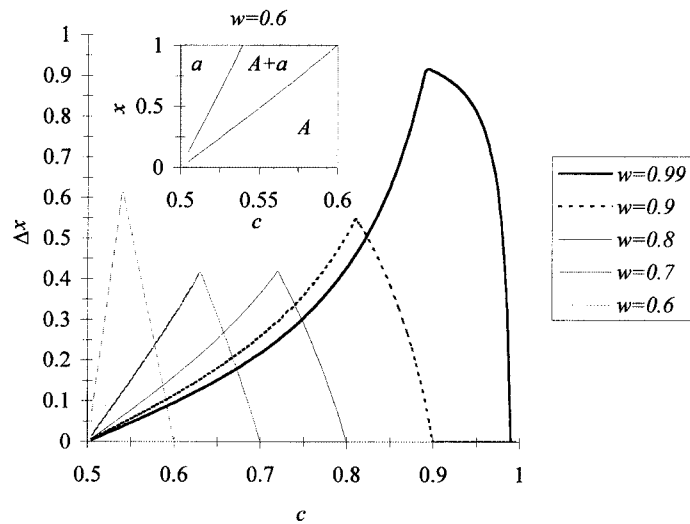


Fig. 4. The window's width ($\Delta x = x_s - x_i$) of soft-regulation rates (intra-niche density dependence) allowing maintenance of polymorphism as a function of c for different values of w ($b = 0.1$). Co-existence is favoured by an increase of c and w . The discontinuities occur when the upper bound (x_s) reaches 1 (a detailed example is given for $w = 0.6$). Note that extreme specialists ($w = 0.99$) exploiting extremely uneven resources ($c = 0.9$) can co-exist under almost all possible kinds of regulation ($\Delta x \approx 0.9$).

This double inequality can be reduced to $(w_A - w_a)(c - w_a) > 0$ for A to be protected when rare and $(w_A - w_a)(c - w_a) \geq 0$ for A not to be invaded when frequent. This is always true if $w_A \leq c \leq w_a$.

It follows that a genotype \hat{A} displaying $w_1(\hat{A}) = c$ and $w_2(\hat{A}) = 1 - c$ cannot be invaded and is always protected in soft-regulated populations. Thus, the relative habitat productivities define completely the degree of specialization that a soft-regulated population can reach (i.e. absolute adjustment). Under hard regulation, the mean fitness of a genotype \hat{A} , $c \cdot w_1(\hat{A}) + (1 - c) \cdot w_2(\hat{A})$, will be maximized for maximum survival in the most frequent habitat, and thus will be the lowest in the less frequent one; namely, if $c > 1/2$, $w_1(\hat{A}) = 1$ and $w_2(\hat{A}) = 0$ (for a linear trade-off).

In the mixed model, genotype \hat{A} cannot be invaded if (from inequality 2) $E_2 \leq 1$ (i.e. a is never protected). Under (3), this expression can be simplified in the following way:

$$(w_A - w_a)[xc(1 - c)(2w_A - 1) - w_A(1 - w_a)(2c - 1)] \leq 0$$

For $c > 1/2$, this inequality is always true, if and only if:

$$w_A = w_{\hat{A}} = \frac{\sqrt{[xc(1 - c)]^2 + (c - \frac{1}{2})^2} - xc(1 - c) + c - \frac{1}{2}}{2(c - \frac{1}{2})}$$

It is easy to show that the ESS \hat{A} is always protected against any other genotype when rare, and that its survival always lies in the interval $[0.5 \dots 1]$. Thus, an unremovable monomorphic state always exists. The best genotype \hat{A} in the mixed model is between that of soft and hard optima. It implies that specialization is more favoured than in soft regulation. However, very little soft regulation is sufficient to move the fitness of the invasive ESS genotype far from the hard-regulated one (Fig. 5).

Model 2

At an ecological time-scale, the conditions for protected polymorphism are only slightly affected for the symmetrical case or the asymmetrical case:

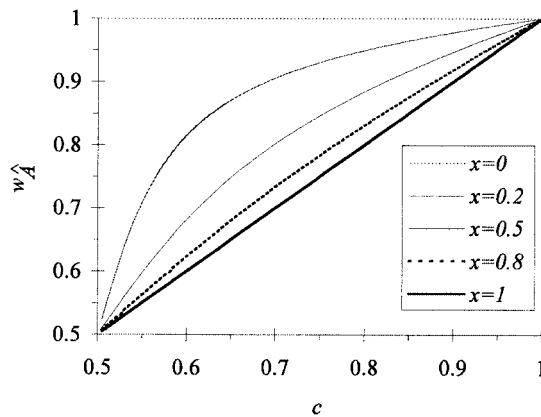


Fig. 5. Survival ($w_{\hat{A}}$) of the invasive ESS (unremovable and protected) genotype as a function of habitat frequency (c) and for different amounts of soft regulation (x).

$$\frac{1-s}{2(1-s)+xs} < c < \frac{1-s+xs}{1(1-s)+xs} \quad (\text{symmetrical case}) \text{ (Fig. 6)}$$

$$\frac{w_a[1-(1-x)w_a]}{x+2w_a(1-w_a)(1-x)} < c < \frac{w_A[1-(1-x)w_A]}{x+2w_A(1-w_A)(1-x)} \quad (\text{asymmetrical case with trade-off}) \text{ (Fig. 7)}$$

At the evolutionary scale, the ESS is closer to pure soft regulation than in model 1 and corresponds to:

$$w_A = w_{\hat{A}} = \frac{\sqrt{x^2c(1-c) + (c - \frac{1}{2})^2} - xc + c - \frac{1}{2}}{2(1-x)(c - \frac{1}{2})} \quad (\text{Fig. 8})$$

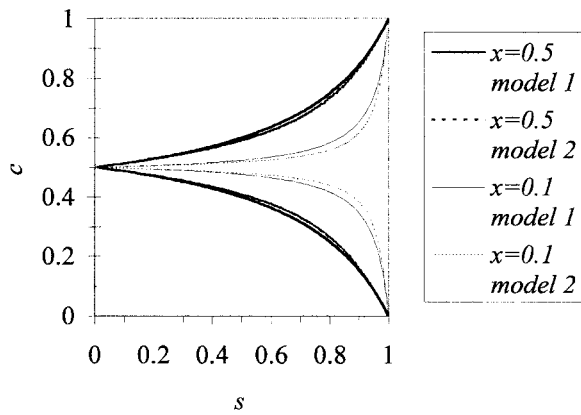


Fig. 6. Comparison of models 1 and 2 for the symmetrical fitness pattern, as in Fig. 2.

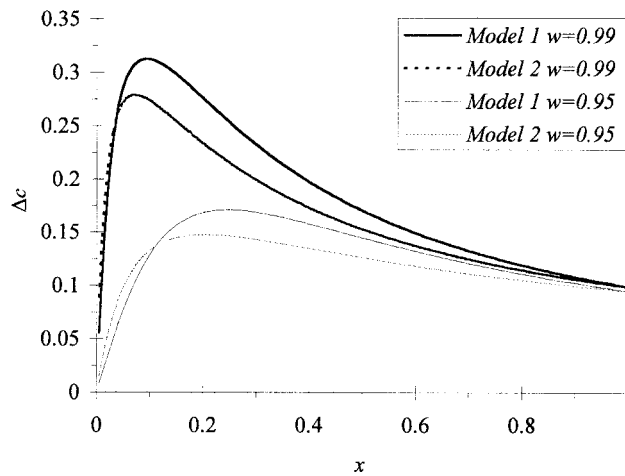


Fig. 7. Comparison of models 1 and 2 for the asymmetrical case, as in Fig. 3.

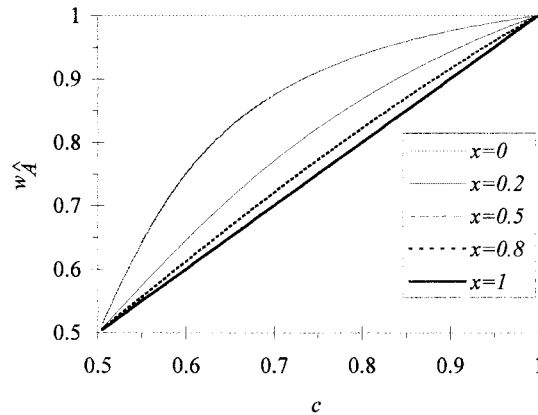


Fig. 8. Invasive ESS obtained with model 2, as in Fig. 5.

In model 2, the contribution of the soft-regulated environment is:

$$\frac{x}{x + (1 - x)(\bar{W}_1 + \bar{W}_2)}$$

which is always higher than in model 1, for which it is simply x . This means that soft regulation will have a greater influence in model 2 than in model 1.

DISCUSSION

The emergent property that mixed models can extend the conditions for maintenance of polymorphism at an ecological time-scale, when compared to the pure soft-regulation case, is a consequence of opposing forces acting in each of the two modes of regulation. As shown in Fig. 9, pure hard selection always tends to protect specialized genotypes, whereas under the same environmental conditions, pure soft selection tends to favour the less specialized genotypes. As specialization increases, soft selection will tend to protect the less specialized genotype much more efficiently than hard selection will for the most specialized one (Fig. 9). This explains why low levels of soft regulation are the most favourable conditions for these two forces to equilibrate. As suggested by Futuyma and Moreno (1988) and confirmed by de Meeûs *et al.* (1993), hard selection better promotes the evolution of habitat specialization.

The maintenance of two slightly differentiated adaptive morphs, exploiting two different resources, is more readily obtained in environments where one resource is far more readily available (or productive) than the other (in our case $c \geq 0.5$) and for which the regulation is mainly hard ($x < 0.5$) (Figs 3 and 4). Otherwise, for c close to 1/2, generalist strategies (generally one) will prevail (Figs 2 and 4).

These patterns should be sought in relevant species with highly dispersive propagules and which exploit a coarse-grained distributed and variable resource. Many parasites (parasitic copepods: Kabata, 1981; Raibaut, 1985; de Meeûs *et al.*, 1990), marine species (polychaetes: Doyle, 1975; bivalves: Bayne, 1976; ascidians: Stoner, 1994) and species producing a large number of highly dispersible propagules (procaryotes, fungi, plants, protozoa) (e.g. Bazzaz, 1991, for plants) may exhibit these features. In host-parasite systems, aggregation of

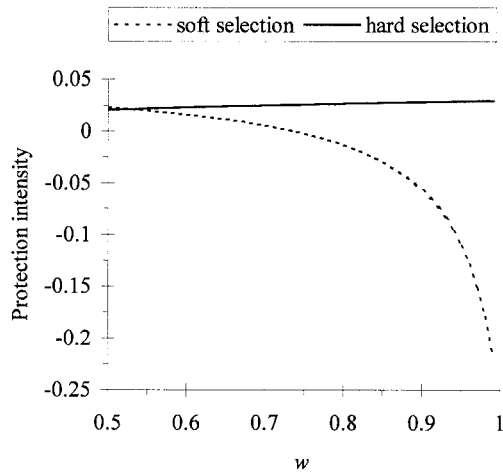


Fig. 9. Illustration of the conflict between soft and hard regulation. Protection intensity of allele A in pure hard (as opposed to pure soft) selection as a function of the extent of specialization (w). Above 0 allele A is protected, whereas below 0 it is selected against. The frequency of habitat 1 is $c = 0.7$ and the extent of de-specialization of allele a is $b = 0.05$.

parasites on their hosts implies that some of the hosts will carry a lot of parasites (saturated hosts) whereas most remain weakly or non-parasitized (unsaturated). Here x is below 0.5 because saturated hosts are in a minority. Hosts may vary in quality (e.g. different genotypes/species), corresponding to favourable conditions for protected polymorphism. Unfortunately, since very low intra-niche density dependence (e.g. $x = 0.1$; Fig. 3) provides the most favourable conditions for the maintenance of polymorphism, evidence for this phenomenon with its consequences on the structuring of populations (or communities) will be difficult to gather. An important feature of our model and of all models of haploid maintenance of polymorphism is that they apply to genes as well as to phenotypes or species.

Our results show that adaptive diversity will be very difficult to maintain at an evolutionary time-scale (long term) in Levene-type models, because an ESS will always eventually invade the environment. This is true for any kind of fitness pattern (trade-off or no-trade off) or regulation (hard to soft regulation). In other words, simple Levene type models cannot account for the maintenance of adaptive diversity in the long term. However, temporal variation of the parameters x or c (defining the environment) could soften this pessimistic view. More importantly, the evolution of habitat preference should modify our findings (Maynard-Smith, 1966; Rosenzweig, 1987, 1991; de Meeüs *et al.*, 1993).

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