

The Tangled Bank: The maintenance of sexual reproduction through competitive interactions

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Abstract

The maintenance of sexual reproduction is discussed using a model based on the familiar Lotka-Volterra competition equations. Both the equilibrium and the stability conditions that allow a sexual population to resist invasion by a single asexual clone are considered. The equilibrium conditions give results similar to previous models: When the cost of sex, within phenotype niche width, and environmental variance are low, the sexual population coexists with the asexual clone and remains at a high density. However, the asexual clone is never completely excluded. Analysis of the stability conditions shows a different picture: The introduction of an asexual clone considerably reduces the stability of the community. However, owing to its larger total niche width, the sexual population exists partly in a “competitor-free space” where the asexual clone has almost no influence on the outcome of the interactions. Therefore the asexual clone is less stable than the sexual population and has a higher probability of extinction. In contrast, the sexual population does not become extinct, since the extreme phenotypes remain at a stable, though low, density, and the central phenotypes, where stability is low, are recreated every generation through recombination. I therefore conclude that the ecological conditions under which sexual reproduction is favored over asexual reproduction are fairly easily attained and are more general than previous analyses had suggested.

Introduction

Why does sexual reproduction persist despite the apparent selective disadvantage of investing in male function? This question has attracted much attention in recent years and several theories have been advanced to explain the apparent paradox (see Bell, 1982 for a review). Some of these theories involve competitive interactions in heterogeneous environments. However it is not yet clear in what manner and to what extent competition reduces the disadvantages of sexuality.

Most recent competition models (e. g. Williams, 1975; Maynard Smith, 1976) are based on the concept of “sib competition”. Consider a heterogeneous environment that contains several different patches, each of which can support at most one individual. When several individuals compete in the same patch, only the one individual that is best adapted to the patch will survive. Now, if a parent does not distribute her offspring to several different patches, but lets them compete against each other and against offspring of other parents in the same patch, then a sexual parent has a higher probability of having the one offspring that is best adapted to the patch in question, and thus has a higher probability of leaving a surviving offspring. Maynard Smith (1976, 1978) presented a precise computer simulation of this situation, and Taylor (1979) and Bulmer (1980) studied his model analytically. Their results show that sexual organisms can indeed have an advantage over asexuals by increasing the probability that some of their offspring are well adapted. However, the conditions that allow the sexual to overcome a twofold cost are very restricted: competition must be very severe, number of offspring must be high, and all offspring of a given parent must compete in one patch. Furthermore, patches must differ in quality, and parents must choose patches randomly, so that no local adaptation to a given patch can occur.

As Young (1981) and Bell (1982) have suggested, these models could more appropriately be called “Lottery Selection Models” to distinguish them from models of the more familiar form of density-dependent competition involving common use of a limiting resource. Ghiselin (1974) first proposed a theory to explain the maintenance of sexual reproduction through density-dependent interactions. His model, which Bell (1982) later called the Tangled Bank, is based on the idea that genetic diversity leads to ecological diversity, so that a sexually produced sibship can exploit a complex environment more efficiently than a genetically uniform asexual sibship (Fig. 1). Thus, if the environment contains a wide array of resources, a single clone can utilize and compete for only a limited portion of the resources. The offspring of a sexual parent, in contrast, utilize a much greater portion of the resources and thus reduce competition among themselves. Although the concept is appealing, only Bell (1982) and Case and Taper (1986) have studied it in any detail. Both studies are simulations. Their results show that competitive interactions can indeed help to maintain sexual reproduction. Bell’s main conclusions are that sexuals can outcompete asexuals if strong genotype \times environment interactions occur and if the environment is heterogeneous and coarse-grained (Bell, 1985). In contrast, Case and Taper (1986) show that, even if the environment is fine-grained, it is possible for sexuals to outcompete asexuals if the niche width of the sexual population is larger than that of the asexual clones. Their model is based on explicit equations for the resource dynamics. They suggest that the explicit modelling of a particular sort of resource dynamics allows the sexuals to survive.

Case and Taper’s (1986) simulation considered only populations in equilibrium, and Bell’s (1982) study considered non-equilibrium conditions by focussing on changing environments and random extinctions. However, as Ghiselin (personal communication) emphasizes, an asexual clone, due to its resource-specialization and its higher rate of increase, might overexploit its resources more readily than a sexual

population. The asexual population might crash even when its equilibrium density is greater than the sexual population's, and when the environment is constant. It is thus necessary to consider the dynamics of the competitive system in addition to the equilibrium conditions.

The purpose of this paper is to generalize the competitive interactions in these models and to give analytical results for the conditions that allow a sexual population to resist invasion by a single asexual clone. Both the equilibrium conditions and the dynamics of the system are considered. Throughout the paper I consider situations which are intrinsically advantageous for the asexuals: using only one resource axis,

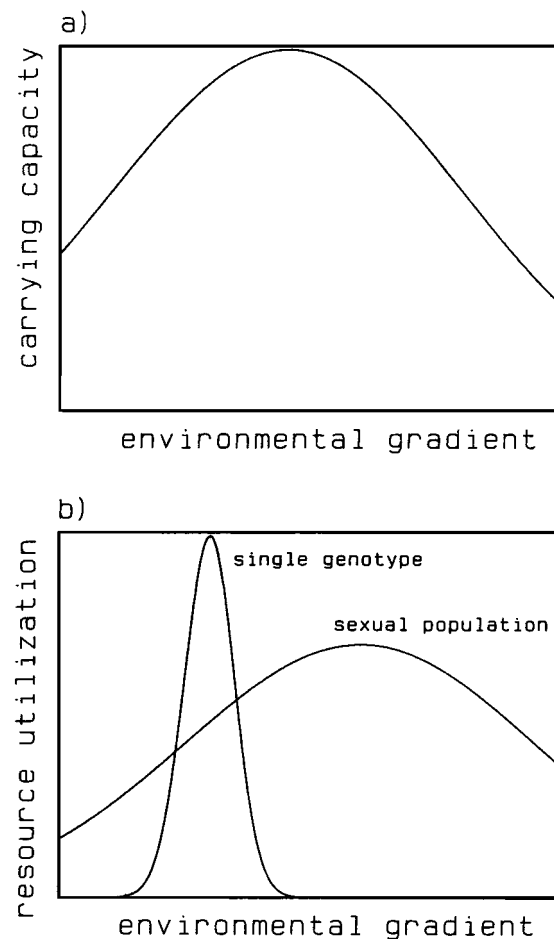


Fig. 1. Schematic representation of the concepts incorporated in Ghiselin's (1974) model of the Tangled Bank. a) Carrying capacity of the environment as a function of the environmental trait. b) Resource utilization of a single clone and of a sexual population as a function of the environmental trait. In contrast to a single genotype, whose resource utilization is restricted, a sexual population can utilize a large range of the available resources.

considering competition of the sexuals against the asexual genotype best adapted to the environment, using a fine-grained environment in which the sexuals cannot disperse to more favorable patches, and assuming only random mating of the sexuals. The results should therefore be interpreted as giving conservative limits for the maintenance of sexual reproduction.

Description of the model

The model describes the coevolutionary outcome of competition for a limiting resource between a sexual, hermaphroditic population and an asexual clone. For convenience the asexual clone and the sexual population will each be referred to as a species. The asexuals arise from sexual organisms by mutation of only the reproductive system and thus are ecologically identical to the sexuals apart from the cost of sex discussed below. To model competitive interactions for a resource, one must map the phenotypic character, z , onto a position on the resource axis, x . Since the fitness and resource utilization of any given phenotype are assumed to decay from their highest values on the resource axis in either direction along the resource gradient, it is convenient to translate the phenotypic value onto the resource axis at the peak of its utilization curve. For example, if competition within a bird species for seeds of different sizes is considered, and the size of seed, say x_0 , that a given bird prefers depends on the length of its bill, say z' , then the bill length is transformed so that its value is equal to the size of seed it prefers, i. e. $z' = x_0$.

Life-History: The organism modelled is hermaphroditic. It has discrete, non-overlapping generations. All individuals encounter identical environmental conditions. Selection occurs only through competitive interactions, and it is assumed that the strength of competition between two individuals depends only on the two phenotypes involved. After selection, the sexuals mate randomly, and each sexual produces an identical number of offspring. The asexuals have more offspring and the offspring are genetically identical to their parent, i. e. no mutations are considered.

Ecology: Competition is modelled using an extension of the Lotka-Volterra equations (Roughgarden, 1979; Milligan, 1986) that describe competition among phenotypes for a limiting amount of resources. This model has been extensively used to describe exploitative competition for resources (e. g. Taper and Case, 1985). Writing W for fitness, the recursion for population size of species i , N_i , is

$$\begin{aligned} N_i(t+1) &= \bar{W}_i N_i(t) \\ \bar{W}_i &= \int p_i(z, t) W_i(z, t) dz \\ W_i(z, t) &= 1 + r_i - \frac{r_i}{K_i(z)} \sum_m N_m(t) \int \alpha_{im}(z, z') p_m(z', t) dz' . \end{aligned} \quad (1)$$

Here $p_i(z, t)$ represents the distribution of phenotype z of species i at time t , $K_i(z)$ denotes the carrying capacity of phenotype z , and r_i denotes the intrinsic rate of increase of species i , i. e. the rate of population growth when density is near 0. The competition function $\alpha_{ik}(z, z')$ represents the effect of a phenotype z' of species k on phenotype z of species i , and is assumed to be independent of the species, i. e. $\alpha_{im}(\cdot) = \alpha_{mi}(\cdot) = \alpha_{ii}(\cdot) = \alpha(\cdot)$. Thus $N_m(t) \int \alpha(z, z') p_m(z') dz'$ is the average effect of species m on a phenotype z , and the sum of this integral represents the combined effect of all competing individuals on a given individual of phenotype z .

The two major components that influence fitness are the competition function $\alpha(z, z')$ and the carrying capacity $K_i(z)$. Assuming a Gaussian distribution of interaction effects between phenotypes z and z' the competition function can be written as

$$\alpha(z, z') = \exp \left(- \frac{(z - z')^2}{2\sigma_a^2} \right) \quad (2)$$

where σ_a is the within phenotype niche width (Roughgarden, 1972; Case and Taper, 1986). Carrying capacity $K_i(z)$ represents the equilibrium population size of species i and phenotype z . It is given by

$$K_i(z) = \int U_i(z | x) R(x) dx \quad (3)$$

where $U_i(z | x)$ represents the utilization of resource x by phenotype z and $R(x)$ is the resource distribution (Milligan, 1986). If it is assumed that the resource utilization by phenotype z is Gaussian with mean x and variance σ_u^2 , and that the resources are normally distributed with mean \bar{x} and variance σ_x^2 , then carrying capacity becomes

$$K_i(z) = \frac{K_{0,i}}{\sqrt{2\pi(\sigma_u^2 + \sigma_x^2)}} \exp \left(- \frac{(z - \bar{x})^2}{2(\sigma_u^2 + \sigma_x^2)} \right)$$

or, with $\sigma_K^2 = \sigma_u^2 + \sigma_x^2$,

$$K_i(z) = \frac{K_{0,i}}{\sqrt{2\pi\sigma_K^2}} \exp \left(- \frac{(z - \bar{x})^2}{2\sigma_K^2} \right) \quad (4)$$

Genetics: Phenotypes are represented by a continuous quantitative character determined by many loci each of small effect. It is assumed that the character is normally distributed with mean \bar{z} and phenotypic variance $V_P = V_a + V_E$, where V_a denotes the additive genetic variance and V_E denotes the environmental variance. This agrees with the empirical observation that many quantitative characters of ecological importance can be characterized by a normal distribution (Falconer, 1981). The evolution of such a trait can be modelled by the standard procedures developed by Lande (1976, 1977), so that the mean phenotype and additive genetic variance evolve according to the equations given by Taper and Case (1985):

$$\begin{aligned}\bar{z}(t+1) &= \bar{z}(t) + h^2(z_w(t) - \bar{z}(t)) \\ V_a(t+1) &= \left(1 - \frac{h^2}{2}\right) V_a(t) + \frac{h^4}{2\bar{W}_s} \int (z - z_w(t))^2 p_s(z, t) W_s(z, t) dz\end{aligned}\quad (5)$$

where the subscript s denotes the sexual species,

$$z_w(t) = \frac{\int z p_s(z, t) W_s(z, t) dz}{\bar{W}_s}$$

is the mean phenotype after selection, and

$$h^2 = \frac{V_a(t)}{V_a(t) + V_E}$$

is the heritability of trait z . It is assumed that the environmental variance, V_E , cannot evolve. Other assumptions implicit in equations (5) include random mating, linkage equilibrium between all loci, no mutation, and the maintenance of a Gaussian phenotype distribution by selection.

As it is assumed that no mutations occur, the asexual clone cannot evolve, and the distribution of phenotypes is determined by

$$p_a(z) = \frac{1}{\sqrt{2\pi V_E}} \exp\left(-\frac{(z - \Delta)^2}{2V_E}\right) \quad (6)$$

where the subscript a denotes the asexual clone, Δ is the mean phenotype of the clone, and the environmental variance, V_E , equals the sexual's.

Cost of sex: The cost of sex, γ , is incorporated in the model by increasing the intrinsic rate of increase, r , and the carrying capacity, K , of the asexuals by a factor γ , i. e. $r_a = \gamma r_s = \gamma r$ and $K_{0,a} = \gamma K_{0,s} = \gamma K_0$. The rationale of this approach is twofold. 1) Because the parthenogenetic clones must not invest in male function, they increase more rapidly than the sexuals when densities are low. 2) Because the parthenogenetic clone only invests resources in female function, a given amount of resources can support a higher density of reproducing individuals. This second point may be more apparent in a dioecious population: Since in an asexual clone, resources must not be shared with males, more females can be supported by a limited amount of resources. Note that the effects of cost of sex are assumed to be identical for rate of increase and for carrying capacity. The qualitative results of the model, however, are not affected by this assumption.

Therefore the major factors that determine the outcome of competition are 1) the mean phenotypes of the two species, i. e. their mean positions on the resource axis, 2) the within-phenotype niche width, i. e. the range of resources utilized by an individual member of the species, 3) the between-phenotype niche width, i. e. the dispersion of different phenotypes' resource utilizations, which is equal to the total niche width of the species minus the within-phenotype niche width, and 4) the cost of sex.

Results of the model

For all of the following results, the asexual clone is assumed to be centered on the resource gradient where its fitness is highest. Therefore the mean environmental condition, \bar{x} , and the mean phenotype of the asexuals can be assumed to be 0 without reducing the generality of the results.

1. Equilibrium conditions

Sexuals alone: As shown by Slatkin (1979, 1980), the sexual population evolves to the following equilibrium

$$\begin{aligned}\hat{N}_s &= \frac{K_0}{\sqrt{2\pi\sigma_a^2}} \\ \bar{z} &= 0 \\ V_P &= V_a + V_E = \sigma_K^2 - \sigma_a^2\end{aligned}\quad (7)$$

if $\sigma_K^2 - \sigma_a^2 > V_E$, otherwise V_a evolves to 0. Several simulations of the model confirmed this result.

One asexual genotype alone: Setting the asexuals' mean fitness

$$\bar{W}_a = 1 + \gamma r - r N_a \int \frac{p_a(z) \int \alpha(z, z') p_a(z') dz'}{K(z)} dz = 1$$

with the mean phenotype at 0 leads to the equilibrium density

$$\hat{N}_a = \frac{\gamma K_0}{\sqrt{2\pi\sigma_K^2}} \sqrt{1 + \frac{V_E}{\sigma_a^2} \left(2 - \frac{\sigma_a^2}{\sigma_K^2} - \frac{V_E}{\sigma_K^2} \right)}. \quad (8)$$

Sexuals and asexual clone in competition: Since the asexual clone is centered at $\Delta = 0$, the sexual population will also evolve towards $\bar{z} = 0$, as was shown for a similar competition model by Case and Taper (1986) and confirmed by several simulations of this model. With $\bar{z} = 0$ and the asexual clone centered at $\Delta = 0$, equations (1), evaluating the integrals, can be written as

$$\begin{aligned}\bar{W}_a &= 1 + \gamma r - r \frac{N_a}{K_{aa}} - r \frac{N_s}{K_{as}} \\ \bar{W}_s &= 1 + r - r \frac{N_a}{K_{sa}} - r \frac{N_s}{K_{ss}}\end{aligned}\quad (9)$$

with

$$K_{aa} = \frac{K_0}{\sqrt{2\pi\sigma_a^2}} \sqrt{\delta + \varepsilon(2 - \delta - \varepsilon)}$$

$$K_{as} = \frac{K_0}{\sqrt{2\pi\sigma_a^2}} \sqrt{\delta + \varepsilon(2 - \delta - \varepsilon) + \varrho(1 - \varepsilon)}$$

$$K_{sa} = \frac{K_0}{\sqrt{2\pi\sigma_a^2}} \sqrt{\delta + \varepsilon(2 - \delta - \varepsilon) + \varrho(1 - \delta - \varepsilon)}$$

$$K_{ss} = \frac{K_0}{\sqrt{2\pi\sigma_a^2}} \sqrt{\delta + \varepsilon(2 - \delta - \varepsilon) + \varrho(2 - \delta - 2\varepsilon - \varrho)}$$

and

$$\delta = \frac{\sigma_a^2}{\sigma_K^2}$$

$$\varepsilon = \frac{V_E}{\sigma_K^2}$$

$$\varrho = \frac{V_a}{\sigma_K^2}$$

Setting $\bar{W}_a = \bar{W}_s = 1$, equations (9) lead to the equilibrium conditions for population density

$$\hat{N}_a = \gamma K_{aa} - \frac{K_{aa}}{K_{as}} \hat{N}_s$$

$$\hat{N}_s = K_{ss} - \frac{K_{ss}}{K_{sa}} \hat{N}_a \quad (10)$$

These equations define a standard Lotka-Volterra equilibrium, so that sexuals and asexuals will coexist only if

$$\gamma K_{aa} < K_{sa}$$

and

$$\gamma K_{as} > K_{ss}$$

or

$$\gamma^2 < \frac{\delta + \varepsilon(2 - \delta - \varepsilon) + \varrho(1 - \delta - \varepsilon)}{\delta + \varepsilon(2 - \delta - \varepsilon)} \quad (11a)$$

$$\gamma^2 > \frac{\delta + \varepsilon(2 - \delta - \varepsilon) + \varrho(2 - \delta - 2\varepsilon - \varrho)}{\delta + \varepsilon(2 - \delta - \varepsilon) + \varrho(1 - \varepsilon)} \quad (11b)$$

Otherwise, if (11a) is not satisfied, the asexual clone will outcompete the sexual population, and if (11b) is not satisfied, the sexual population will win. However, for $V_P = V_a + V_E > \sigma_K^2$, which is always true at equilibrium (see below), condition (11b) is

never met for $\gamma > 1$, and the sexual population can never be fixed, i. e. the sexuals can never completely eliminate the invading clone.

At equilibrium, equations (5), together with equations (1) and $V_a(t+1) = V_a(t)$ lead to the implicit equation for phenotypic variance at equilibrium shown in the appendix. It can be shown that this equilibrium variance is defined only if

$$\frac{V_p}{\sigma_K^2} = \varrho + \varepsilon < 1 - \frac{\delta}{2} + \sqrt{1 + \frac{\delta^2}{4}}. \quad (12)$$

The conditions for coexistence and the equilibrium variance are depicted in Fig. 2. The proportion of sexuals in the population at equilibrium can be calculated from equation (10) as

$$\frac{\hat{N}_s}{\hat{N}_s + \hat{N}_a} = \frac{K_{ss} \left(1 - \gamma \frac{K_{aa}}{K_{ss}} \right)}{K_{aa} \left(\gamma - \frac{K_{ss}}{K_{aa}} \right) + K_{ss} \left(1 - \gamma \frac{K_{aa}}{K_{sa}} \right)}. \quad (13)$$

This proportion is depicted in Figs. 3 and 4 for various values of within-phenotype niche width, environmental variance, and cost of sex. Coexistence of a sexual population and an asexual clone is possible for a limited range of the parameter space, confirming Bell's (1982) results. However, it seems that Case and Taper's (1986) optimistic results are due to their extreme parameters (their V_E/σ_K^2 and σ_a^2/σ_K^2 are on the order of 0.001, which correspond to the lower left corner of Fig. 3).

2. Stability

As is well known (e. g. May, 1972) for Lotka-Volterra dynamics the system is stable when growth is continuous, but can become unstable with discrete generations when r , the intrinsic growth rate, exceeds two, and a population regulated by Lotka-Volterra competition shows chaotic behavior when r exceeds three. These conditions change when several species compete and are further complicated when genetics are considered.

Here I describe the stability conditions for a sexual and an asexual species in competition when mean phenotype and genetic variance of the sexual species are fixed at their equilibrium values. The procedure closely follows May (1972). Thus small deviations from the equilibrium condition are considered by setting

$$N_i(t) = \hat{N}_i(1 + v_i(t))$$

and

$$V_a(t) = \hat{V}_a.$$

Then the Lotka-Volterra equations are reduced to

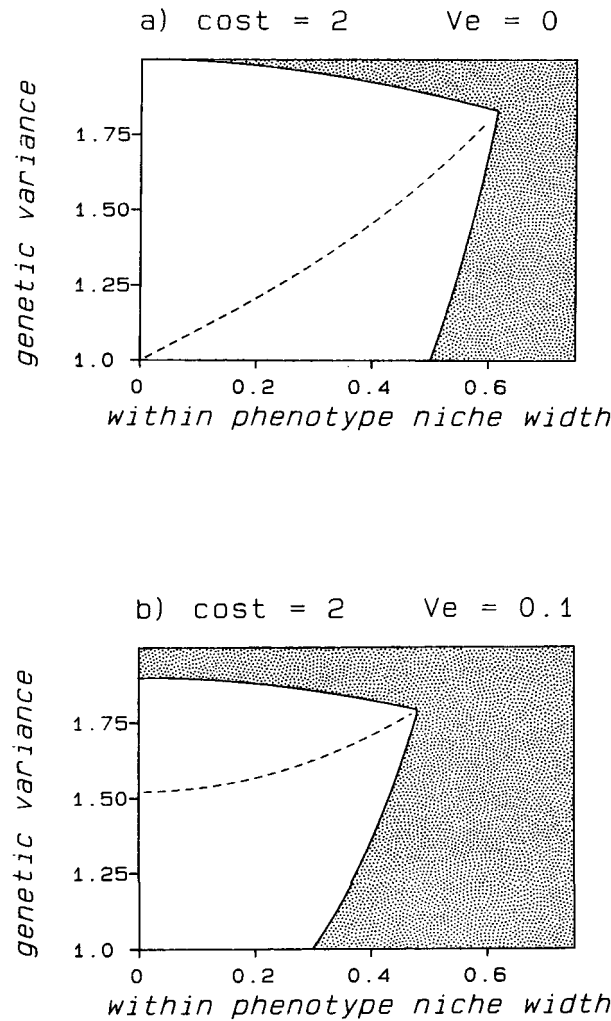
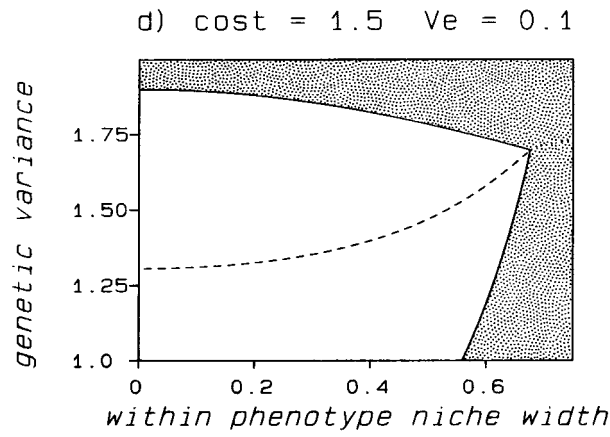
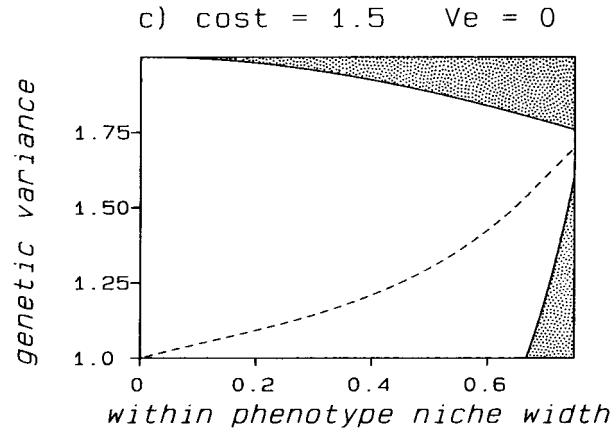


Fig. 2. Equilibrium condition for a sexual population in competition with an asexual clone for various costs of sex and environmental variances. Since the mean value of the environment and the mean phenotype of the asexual clone are zero, the mean phenotype of the sexual population is also zero and is not depicted. The genetic variance at equilibrium, \hat{V}_a/σ_k^2 , (dashed line) is shown as a function of the within phenotype niche width σ_x . In the stippled area, the asexual clone outcompetes the sexual population. Note that the genetic variance of the sexual cannot exceed a value determined by the within-phenotype niche width. The four panels show different values of the parameters γ (cost of sex) and V_E (environmental variance). a) $\gamma = 2$, $V_E = 0$; b) $\gamma = 2$, $V_E = 0.1\sigma_k^2$; c) $\gamma = 1.5$, $V_E = 0$; d) $\gamma = 1.5$, $V_E = 0.1\sigma_k^2$.



$$v_a(t+1) - v_a(t) = -r \frac{\hat{N}_a}{K_{aa}} v_a(t) - r \frac{\hat{N}_s}{K_{as}} v_s(t)$$

$$v_s(t+1) - v_s(t) = -r \frac{\hat{N}_a}{K_{sa}} v_a(t) - r \frac{\hat{N}_s}{K_{ss}} v_s(t) . \quad (14)$$

The eigenvalues, λ_i , of the right-hand side of these equations are

$$2\lambda_{1,2} = -r \left(\frac{\hat{N}_a}{K_{aa}} + \frac{\hat{N}_s}{K_{ss}} \right) \pm r \sqrt{\left(\frac{\hat{N}_a}{K_{aa}} - \frac{\hat{N}_s}{K_{ss}} \right)^2 + 4 \frac{\hat{N}_a \hat{N}_s}{K_{as} K_{sa}}} . \quad (15)$$

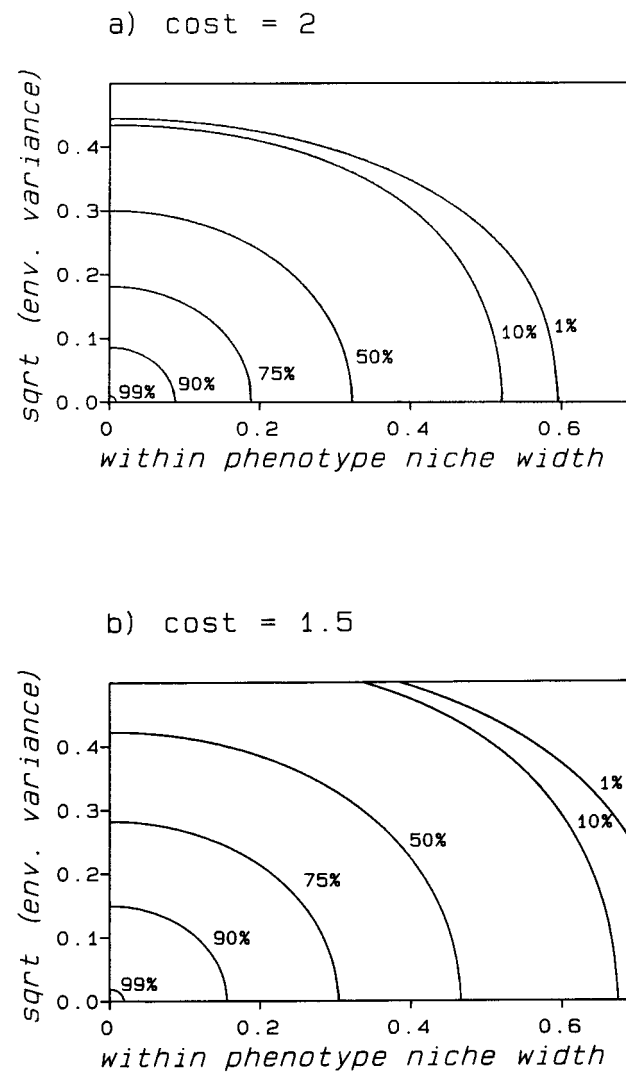


Fig. 3. The percentage of the sexual individuals in the community at equilibrium for a) cost of sex, $\gamma = 2$; b) $\gamma = 1.5$. For the greater portion of the parameter space, the sexual population is restricted to very low densities when competing with even a single clone.

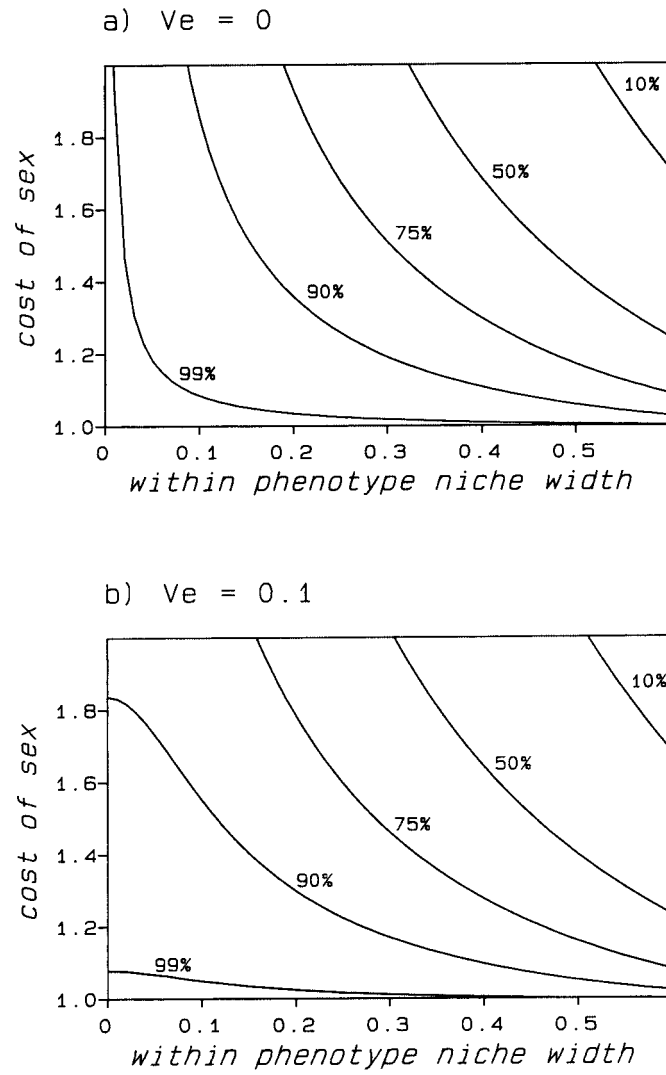


Fig. 4. The percentage of the sexual individuals in the community at equilibrium for a) environmental variance, $V_E = 0$; b) $V_E = 0.1\sigma_k^2$.

Since both of these values are real, the necessary conditions for stability of the system of difference equations are (May, 1972)

$$-2 < \lambda < 0.$$

The second of these conditions, $\lambda < 0$, leads to

$$K_{aa}K_{ss} < K_{as}K_{sa} \quad (16a)$$

which is always satisfied in conditions that allow coexistence, and the first, $\lambda > -2$, leads to

$$r < \frac{4}{\left(\frac{\hat{N}_a}{K_{aa}} + \frac{\hat{N}_s}{K_{ss}}\right) + \sqrt{\left(\frac{\hat{N}_a}{K_{aa}} - \frac{\hat{N}_s}{K_{ss}}\right)^2 + 4\frac{\hat{N}_a\hat{N}_s}{K_{as}K_{sa}}} \quad (16b)$$

The greatest values of r that allow stability for various parameters are shown in Fig. 5. For high costs (rapid growth of asexuals), stability is considerably reduced, whereas the sexual species, when alone, is stable up to $r = 2$. Such a decrease in stability leads to a finite probability of extinction due to chaotic fluctuations of the populations. Though, in principle, chaos could eliminate either the sexual or the asexual species, simulation of competition with high r shows that whenever one of the species disappears, it is the asexual species, whereas the sexual population increases to the equilibrium density given by equation (7) (Fig. 6). Thus, even if the equilibrium density of the asexual is considerably higher than the density of the sexual, the asexual clone is rapidly eliminated. Because the extreme phenotypes of the

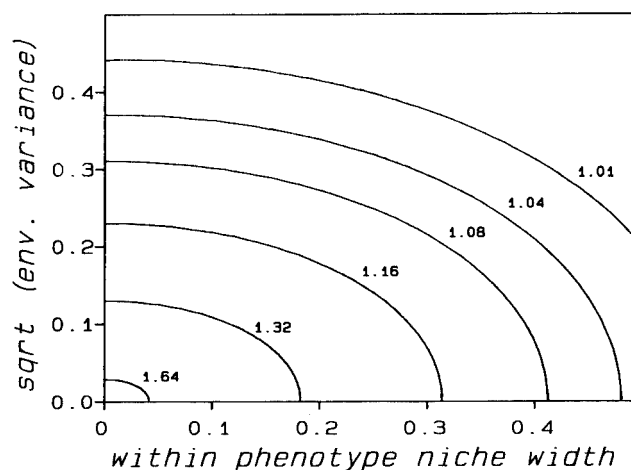


Fig. 5. Conditions for stable coexistence of a sexual population and an asexual clone. Each curve connects those values of environmental variance and within-phenotype niche width that allow stability for the value of r shown next to the curve. Combinations of parameters that lie below the curve lead to stable coexistence, whereas parameters that lie above the curve lead to instability and possibly chaos. Stability is generally considerably reduced when the asexual clone is introduced to the population.

sexual species are not affected by the asexuals, the outer portions of the sexual population's resource distribution remain stable for high rates of increase. Therefore, when the more central phenotypes are eliminated, they are recreated through recombination of the extreme phenotypes. In contrast, all asexual phenotypes are under strong competition with the central sexuals, and when they disappear, they cannot be recreated. Thus the sexual can outcompete the asexual due to constant, though low, fitness in the outer portions of its distribution, and thus low variance in

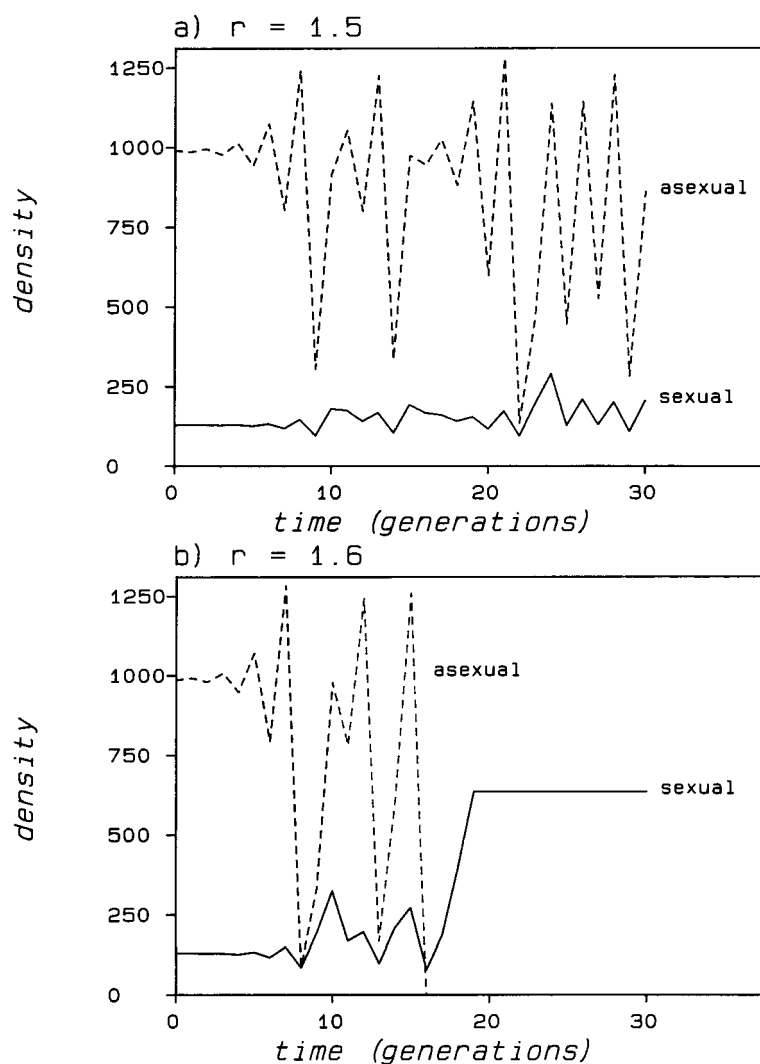


Fig. 6. Two typical examples of the population density fluctuations for sexuals and asexuals. Both panels show the dynamics with the cost of sex, $y = 2$, within-phenotype niche width, $\sigma_a^2 = 0.25\sigma_k^2$, and environmental variance, $V_E = 0.25\sigma_k^2$. a) $r = 1.5$, b) $r = 1.6$. Asexuals show much larger fluctuations, and thus greater variance in fitness, than the sexual population.

fitness for the total population. Although the asexual clone has higher mean fitness, its variance is much larger than that of the sexual population (Fig. 7).

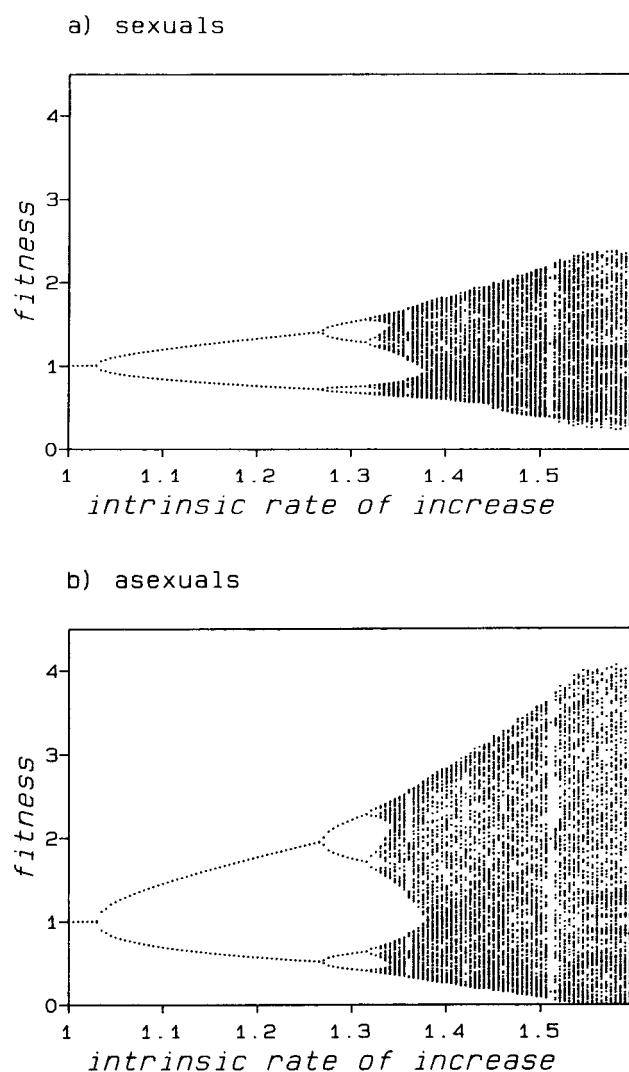


Fig. 7. Plot of mean fitnesses of a sexual population (a) and an asexual clone (b) in competition. The fitnesses are generated by iterating equations (1) for 200 generations for each of a sequence of values of r , using the parameters $\sigma_a^2 = 0.16\sigma_k^2$ and $V_E = 0.0625\sigma_k^2$. The densities were initialized near the equilibrium densities given by equation (10), and the first several generations were omitted in the plots. If the asexual population became extinct before 200 generations, the population was reinitiated close to equilibrium. The plots give an impression of the probability distribution of mean fitnesses over time. It is apparent that the variance in fitness of the asexual clone is much higher than the sexual's variance. Therefore the asexual clone disappears frequently for large values of r .

Discussion

The equilibrium results clearly demonstrate that, as shown by Bell (1982) and Case and Taper (1986), sexuals can overcome their intrinsic disadvantage due to the cost of sex even when the cost of sex is at the maximal value of two. However, the sexual species can never eliminate its asexual competitor. Even under the conditions that restrict a single asexual clone to very low densities, the number of asexual mutants will steadily increase until the sexual is eliminated. Furthermore, the parameter space that allows coexistence is rather restricted in that phenotypic plasticity, i. e. both within phenotype niche width and environmental variance of the considered trait, must be small compared to the variance in the resource distribution. Thus, if only equilibrium effects are considered, it seems that competition cannot explain the maintenance of sexuality in nature. However, the disadvantage of sexuality can be reduced at equilibrium by effects such as non-random mating or dispersal and habitat choice. These processes let the sexuals reduce competition with the asexuals, either by evolving phenotypes that differ from the asexuals' or by selecting habitats where the asexual is inefficient. Furthermore, the effects of competition on the sexual population when the populations are not in equilibrium can be much greater than the equilibrium effects. Such non-equilibrium effects can be found in changing environments (Bell, 1982) or in the dynamics intrinsic to the system as discussed in this paper.

As Bell (1982) notes, changes in the environment will change the distribution of the carrying capacity function. In particular two effects can be seen to aid the sexuals in eliminating their asexual competitors: 1) If the mean of the carrying capacity function fluctuates, the asexual genotype is only rarely competing in an optimal environment. It may not be able to increase in density and may even be eliminated. 2) If the carrying capacity for a given environment fluctuates, then it may reach zero in the portion of the resource gradient occupied by the asexual clone, and the clone will be eliminated. Thus, year-to-year fluctuations in climate, pests, etc. can destabilize the populations, so that the geometric mean fitness of the sexuals exceeds that of the asexuals.

An effect that does not depend on random fluctuations of the environment or random extinctions is seen in the dynamics of the community. The introduction of an asexual competitor considerably reduces the stability of the system. For high intrinsic rates of increase, the system becomes chaotic, which eventually leads to the extinction of the asexual competitor. The sexuals are never eliminated since, by virtue of their greater phenotypic variance, they occupy a greater proportion of the environment and utilize a greater proportion of the resources. Many of the extreme individuals therefore occupy a "competitor-free" space, where the effect of the asexual competitor is negligible. These individuals have low mean fitness, but their variance in fitness over time is also very low. Only the central phenotypes show the instability introduced by the asexuals. Thus asexuals and central sexual phenotypes, due to their high variance in fitness, are eliminated through their chaotic behavior. This means that the asexual clone will be eliminated from the population, whereas the sexual phenotypes are recreated the next generation

through recombination by the extreme phenotypes. This effect of high vs. low variance in fitness is very strong, and asexuals are eliminated even when the equilibrium density of the asexual clone is much higher than the equilibrium density of the sexuals.

It has been shown mathematically by Gillespie (1974, 1975, 1977) that selection should operate on variance in fitness as well as on mean of fitness: when fitness fluctuates over time, the best measure of fitness is the geometric mean of the offspring number averaged over time. This is approximately $\mu - \sigma^2/2$, where μ is the average number of offspring, and σ^2 is the variance in number of offspring. Both sexuals and asexuals have mean fitness close to one, so that the lower variance in fitness of the sexuals leads to a considerably higher geometric mean fitness. The effect of variance in fitness has also been identified by Stearns (1986), who suggests that sex functions as a risk-minimizing device.

Comparative evidence

A major assumption of the Tangled Bank is that resource utilization and fitness of a genotype depend on the environment in which it is raised. That such interactions frequently occur is well established. In fact, Bell (1985), after reviewing several studies that clearly demonstrate strong genotype-environment interactions, states that “most large-scale studies of variation involving many combinations of strains and treatments turn up substantial interactions”.

Critical for the outcome of competition at equilibrium is the value of within-phenotype niche width. Though a large body of literature exists on this topic, I present two particularly clear examples of limited resource utilization. Gibbons (1979) studied the interactions of *Megarhyssa* (Hymenoptera: Ichneumonidae) with its host-larvae. These larvae burrow in dead wood or stumps, and the depth of an attacked host-larva closely matches the length of the wasp's ovipositor. Since the range of depths occupied by individual larvae varies, a given wasp can parasitize only a small fraction of all available larvae. The proboscis lengths of the bumblebees *Bombus ternarius* and *B. pennsylvanicus* are strongly correlated with the corolla length of the flowers they visit (Johnson, 1986). Individuals with a long proboscis never visit a flower with a short corolla and vice-versa, and the resources utilized by an individual bee are therefore limited.

According to the model, high values of intrinsic rate of increase favor sexual reproduction, whereas, in the absence of environmental fluctuations, low rates of increase favor asexual reproduction. As shown by Blueweiss et al. (1978), intrinsic rate of increase is strongly negatively correlated with body size. This immediately raises the question: Why does sexual reproduction prevail among large, slow-breeding organisms, such as mammals and birds, while small organisms with apparently high rates of increase are often asexual? I will argue that this apparent contradiction is an artefact of the units in which rate of increase is measured. It is critical to note that Blueweiss et al. (1978) measured rate of increase in units of days^{-1} . However, if instability is to be inferred, rate of increase must be measured in $(\text{generation time})^{-1}$.

Blueweiss et al.'s correlation can easily be corrected by noting their correlation of maturation time with body size. They show that $r_{max} \propto W^{-0.26}$ and $\alpha \propto W^{0.27}$, where r_{max} denotes intrinsic rate of increase per day, α denotes maturation time in days, and W denotes body size. Since rate of increase per generation can be approximated by multiplying rate of increase per day with maturation time, rate of increase per generation is obviously not or only very slightly correlated with body size. Thus the observation that asexual reproduction prevails in small organisms does not contradict the model. Furthermore, several studies show that even large, slow-breeding organisms have rather high rates of increase per generation (Table 1). Most of the values cited in Table 1 are sufficiently high to destabilize an invading asexual clone, especially in the light of other destabilizing factors, such as year-to-year fluctuations in climate or pests.

Thus the major assumptions of the model – genotype-environment interaction, small within-phenotype niche width, and sufficiently high intrinsic rate of increase – are well supported. Furthermore, as Bell (1982) has shown, the geographic patterns of distribution of sexual and asexual animal species support the hypothesis that competitive interactions in a saturated and complex environment favor sexuality. More recent data on the distribution of asexual and sexual reproduction in higher plants (Bierzychudek, 1985) show the same geographic pattern. Antonovics and Ellstrand

Table 1. Rates of increase. The cited rate is the rate of increase found in the literature. Rate of increase per generation was calculated by multiplying the cited rate by age at maturity. The rate of increase for a discrete model, λ , was obtained with $e^r - 1 = \lambda$.

Species	cited r^1	corrected λ	References
<i>Accipiter nisus</i>	0.76 y	1.14	Tanner (1975)
<i>Alces americana</i>	0.20 y	0.82	Tanner (1975)
<i>Bos taurus</i>	0.001 m	1.05	Fenchel (1974), Stearns (pers. comm.)
<i>Canis lupus</i>	0.52 y	1.83	Tanner (1975)
<i>Felis concolor</i>	0.49 y	2.40	Tanner (1975)
<i>Gadus morrhua</i>	0.0065 m	0.61	Fenchel (1975), Stearns (unpublished data)
<i>Lepus americanus</i>	1.03 y	1.80	Tanner (1975)
<i>Lynx canadensis</i>	1.01 y	1.75	Tanner (1975)
<i>Macropus fuliginosus</i>	0.53 y	1.23	Bayliss (1985a, 1985b), Russell (1982)
<i>Macropus rufus</i>	0.67 y	1.75	Bayliss (1985a, 1985b), Russell (1982)
<i>Microtus agrestis</i>	0.0126 m	1.21	Fenchel (1974), Stearns (unpublished data)
<i>Mustela vison</i>	0.53 y	0.70	Tanner (1975)
<i>Odocoileus hemionus</i>	0.24 y	0.62	Tanner (1975)
<i>Odocoileus virginianus</i>	0.30 y	0.82	Tanner (1975)
<i>Ondatra zibethica</i>	1.37 y	2.94	Tanner (1975)
<i>Ovis dalli</i>	0.11 y	0.39	Tanner (1975)
<i>Passer domesticus</i>	1.31 y	2.71	Tanner (1975)
<i>Rangifer arcticus</i>	0.20 y	0.49	Tanner (1975)
<i>Rattus norvegicus</i>	0.0148 m	2.17	Fenchel (1974), Stearns (unpublished data)

1: The units are year⁻¹ (y) or month⁻¹ (m).

(1984), Ellstrand and Antonovics (1985), and Schmitt and Antonovics (1986) have published the results of their experimental work on the significance of sexual reproduction. Their data support the predictions of several rival hypotheses, including the Tangled Bank. However, since many hypotheses differ mainly in their assumptions, but not in their predictions, it should be worthwhile to design experiments that specifically test both the predictions and the assumptions of the Tangled Bank.

Summary

Competition for a limiting resource helps a sexual population to resist invasion by reproductively efficient asexual mutants under the following conditions: 1) genotype-environment interaction, i. e. a given genotype must be the best genotype for one resource, but not for others, 2) small environmental variance and within-phenotype niche width, i. e. little phenotypic plasticity, and 3) a fairly high intrinsic rate of increase. In contrast to studies of equilibrium conditions, it is shown that the major mechanism responsible for the exclusion of the asexuals is the greater temporal variance in fitness of the asexuals, and thus the asexuals' lower geometric mean fitness.

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Appendix

The genetic variance of the sexual species at equilibrium can be found by setting

$V_a(t+1) = V_a(t) = \hat{V}_a$ in equation (5) with $\bar{x} = \Delta = \bar{z} = 0$. Thus

$$\hat{V}_a = \int z^2 p_s(z) W_s(z) dz - V_E. \quad (\text{A1})$$

Equation (A1), together with equations (1) at equilibrium, leads to

$$V_P = \hat{V}_a + V_E = \hat{N}_a \int z^2 p_s(z) \frac{\int p_a(z') \alpha(z, z') dz'}{K(z)} dz - \hat{N}_s \int z^2 p_s(z) \frac{\int p_s(z') \alpha(z, z') dz'}{K(z)} dz \quad (\text{A2})$$

and, since in general

$$\frac{1}{\sqrt{2\pi\sigma^2}} \int_{-\infty}^{\infty} (x - \bar{x})^2 \exp\left(-\frac{(x - \bar{x})^2}{2\sigma^2}\right) dx = \sigma^2$$

equation (A2) leads to

$$1 = \frac{\hat{N}_a}{K_{sa}} \frac{\sigma_a^2 + V_E}{\sigma_a^2 + V_E + V_P \left(1 - \frac{\sigma_a^2 + V_E}{\sigma_k^2}\right)} + \frac{\hat{N}_s}{K_{ss}} \frac{\sigma_a^2 + V_P}{\sigma_a^2 + V_P \left(1 - \frac{\sigma_a^2 + V_P}{\sigma_k^2}\right)}. \quad (\text{A3})$$

Together with equations (10) for the equilibrium densities, and using the terms

$$\begin{aligned} \xi &= \delta + \varepsilon(2 - \delta - \varepsilon) \\ A &= \xi + \varrho(2 - \delta - 2\varepsilon - \varrho) \\ B &= \xi + \varrho(1 - \delta - \varepsilon) \end{aligned}$$

(A3) becomes

$$1 = \frac{\gamma - \sqrt{\frac{A}{\xi + \varrho(1 - \varepsilon)}}}{\sqrt{\frac{B}{\xi}} - \sqrt{\frac{A}{\xi + \varrho(1 - \varepsilon)}}} \left(\frac{\delta + \varepsilon}{A} - \frac{\delta + \varrho}{B} \right) + \frac{\delta + \varepsilon}{A} \quad (\text{A4})$$

which can be solved for the equilibrium genetic variance $\varrho = \hat{V}_a/\sigma_k^2$. This can only be done if all terms under the square roots are positive. Since δ and ε are limited to values less than one, it is easily seen that ξ and $\xi + \varrho(1 - \varepsilon)$ are positive, so that equation (A4) can be solved if

$$A = \xi + \varrho(2 - \delta - 2\varepsilon - \varrho) > 0 \quad (\text{A5a})$$

and

$$B = \xi + \varrho(1 - \delta - \varepsilon) > 0. \quad (\text{A5b})$$

Since ϱ always evolves to values greater than one when sexuals compete with asexuals (Fig. 2), equation (A5b) is always satisfied. In contrast, rearrangement of equation (A5a) to

$$\varrho^2 - (2 - 2\varepsilon - \delta)\varrho - (\delta + \varepsilon)(1 - \varepsilon) - \varepsilon > 0$$

shows that equation (A4) can only be satisfied if

$$\varrho + \varepsilon < 1 - \frac{\delta}{2} + \sqrt{1 + \frac{\delta^2}{4}}. \quad (\text{A6})$$