Instability of the sexual continuum

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SUMMARY

Maynard Smith & Szathmari (1995) have posed the problem of demonstrating the conjectured instability of a continuum of sexual types with finite interbreeding. Here, I propose a model in which one can analyse exactly when and how the existence of the instability can depend on an Allee effect, and how the growthrate and typical scale of the unstable perturbations depend on the strength and range of competition, mating preference, fecundity and offspring variance due to Mendelian segregation and mutation. Instabilities of various kinds are shown to occur in the majority of parameter regimes. In short: the continuum often breaks up into incipient species.

1. INTRODUCTION

Maynard Smith & Szathmari (1995) have pointed out some fundamental gaps in our understanding of why sexually propagating populations tend to occur in the form of discriminable and biologically distinct species, whereas asexuals often occur in forms which seem less distinct. After reviewing the data and models relevant to this long-standing problem, the authors draw a useful distinction between: (1) the conjectured instability of a continuum of sexuals which can interbreed across finite genetic distances; and (2) the complementary question of whether new types can invade ‘gaps’ in character-space between existing species or distinct clones.

For asexuals, classic analytical results (e.g. Roughgarden 1979) show that new clones can invade at least the wider of any set of gaps, no matter how small these are compared to the range over which clones compete for resources. Hence, one expects the packing in character-space to become very dense, limited only by stochastic extinction and the fact that the equilibrium distribution depends sensitively on small-scale fitness differences (*vide infra*).

For sexuals, the Allee effect has been proposed (Bernstein *et al.* 1985) to be the crucial factor which causes a continuum of types to break up into species. However, the model (Hopf & Hopf 1985) quoted as support for this notion only refers to instability in the niche packing of pre-specified species with perfect reproductive isolation. Thus, the Hopf & Hopf model cannot answer question (1) above, although it may answer question (2).

As Maynard Smith & Szathmari (1995) point out, a model is required in which instability of a continuum of sexuals with finite-range interbreeding can be studied. In this short paper, I present a model in which this problem can be solved analytically. The question of invasibility and late-stage phenomena in sympatric speciation may also be studied in the model, but this must be deferred to a longer paper.

2. THE MODEL

The stability problem posed by Maynard Smith & Szathmari has the attraction of being both general and simple. In the same spirit, I refrain from incorporating many of the more specialized mechanisms which have been discussed during the long and varied history of the ‘species problem’, without implying that such contributions cannot be important. The results which I obtain here, under conditions which cover many biologically relevant cases, should provide at least a useful ‘baseline’. Other factors might then be shown to add new features, or modify existing ones.

A suitable model can be written down by straightforward accounting for the deaths and (viable fertile) births of individuals of various types; the general approach is analogous to that of an early model (Levin & Segel 1982, 1985) which can be recovered by imposing special restrictive conditions. For simplicity, only one trophic level is considered; others may be considered as being at quasi-steady-state. I also assume a fixed sex ratio (clonal propagation emerges as a special limit), and deterministic dynamics of a continuous population density $N(x) : \mathbb{R}^d \mapsto \mathbb{R}^+$. The argument x represents a d -dimensional, continuous additive fully-heritable character. Thus, x does not include the ‘environmental variance’ σ_e^2 (Roughgarden 1979). The phenotype distribution of the population could be obtained by convolving $N(x)$ with a Gaussian of width σ_e , but such ‘blurring’ does not influence the $N(x)$ -dynamics directly; it merely sets a lower bound on some model parameters defined below. The dynamics of $N(x)$ should have the general form

$$\partial_t N(x) = -D(x)N(x) + B(x), \quad (1)$$

with appropriate expressions for the death rate $D(x)$ and birth count $B(x)$.

Apart from a constant term (set to one), the death rate $D(x)$ must contain a term linear in a blurred version of $N(x)$, to properly represent competition due

to, say, partial overlap of resource-utilization functions. Phenotypic similarity is what counts here, so σ_e sets a lower bound to the blur width. Higher order terms in $D(x)$ may be truncated.

Thus, I write $D(x) = 1 + cg_c \star N(x)$, using

$$g_i \star N(x) \equiv \int_{-\infty}^{+\infty} g_i(\xi) N(x + \xi) d\xi$$

as shorthand notation for convolutions with general kernels $g_i(x)$, all of which are assumed to be Gaussians $g_i(x) = (\sqrt{2\pi}\sigma_i)^{-d} \exp[-|x|^2/(2\sigma_i^2)]$. In particular, $g_c(x)$ is the competition kernel. All integrals are implicitly d -dimensional.

Next, we need to write down $B(x)$, which counts the (viable fertile) births. Consider a female of type $x = \xi_1$ (male and female may be interchanged throughout). She accepts type- ξ_2 males with a preference denoted by the mating kernel $g_m(\xi_2 - \xi_1)$, a Gaussian whose width σ_m may be bounded below by the phenotypically limited discriminability of males. Hence, ξ_1 females perceive a total of $\propto g_m \star N(\xi_1)$ males as eligible for mating. Without an Allee effect, i.e. in very dense populations, the number of matings between ξ_1 females and ξ_2 males would be $\propto N(\xi_1)g_m(\xi_2 - \xi_1)N(\xi_2)/[g_m \star N(\xi_1)]$. To incorporate an Allee effect, this must be multiplied by a saturating function of the number of acceptable mates. Choosing this Allee factor to be $\propto g_m \star N(\xi_1)/[\eta + g_m \star N(\xi_1)]$ yields the simplest final expression. To count the (viable fertile) offspring we need to multiply the mating count by a pair-dependent fecundity, $f(\xi_2 - \xi_1)$, which may also represent any ‘outbreeding depression’. So far then, we have a term proportional to

$$f(\xi_2 - \xi_1)g_m(\xi_2 - \xi_1) \frac{N(\xi_1)N(\xi_2)}{\eta + g_m \star N(\xi_1)} \quad (2)$$

for the births contributed by ξ_1, ξ_2 matings.

Assuming that there is no genetic dominance, the offspring from a ξ_1, ξ_2 mating will have a Gaussian character distribution centred on $x = \frac{1}{2}(\xi_1 + \xi_2)$. The width, σ_v , of this distribution, $g_v(x)$, represents Mendelian segregation plus mutation. We may now compute $B(x)$ by integration over the possible matings and the g_v kernel. The result can be put in a more symmetric form by writing $\xi_{1,2} = x \pm \xi$. This yields

$$B(x) = b(x) \times g_v \star \int_{-\infty}^{+\infty} f(2\xi)g_m(2\xi) \frac{N(x+\xi)N(x-\xi)}{\eta + g_m \star N(x+\xi)} d\xi. \quad (3)$$

Note that all proportionality factors and normalization constants have been absorbed into one effective birth-factor $b(x)$. Finally, the product of Gaussians $f[2\xi]g_m[2\xi]$ is replaced by a single Gaussian $g_f(\xi)$ of width σ_f , which implies the constraint $\sigma_f \leq \frac{1}{2}\sigma_m$. The required normalization of g_f is again absorbed into $b(x)$. Putting everything together, one obtains

$$\partial_t N(x) = -N(x)\{1 + cg_c \star N(x)\} + b(x)g_v \star \int_{-\infty}^{+\infty} g_f(\xi) \frac{N(x+\xi)N(x-\xi)}{\eta + g_m \star N(x+\xi)} d\xi. \quad (4)$$

(a) *Perturbing the uniform continuum*

The question posed by Maynard Smith & Szathmáry concerns speciation in the absence of intrinsic fitness differences, so I specialize to $b(x) = b$. Small $b(x)$ -perturbations are reintroduced when needed. The qualitative results remain essentially unchanged when b depends on x very smoothly.

The analysis starts by finding the uniform equilibria $N(x) = N_0$. Apart from the trivial solution $N_0 = 0$, there are two solutions, say N_0^+ and N_0^- . For reasonably small Allee effects ($\eta \ll (b-1)^2/c$), the exact solutions can be approximated by

$$N_0^+ \approx \frac{b-1}{c} - \eta \frac{b}{b-1}, \quad (5)$$

$$N_0^- \approx \eta \frac{b}{b-1}. \quad (6)$$

The larger solution N_0^+ is the ‘sexual continuum’, while the much smaller solution N_0^- acts as a ‘threshold’ to invasion.

The stability of N_0^+ is determined by studying small perturbations $n(x)$ of this (exact) equilibrium. After linearizing equation (4) around N_0^+ , one may contract $g_v \star g_f$ into one ‘birth’ kernel g_b ; this implies $\sigma_b^2 = \sigma_v^2 + \sigma_f^2$. It then proves useful to rephrase the problem in terms of the Fourier spectrum $s(q)$ of $n(x)$, i.e. $s(q) \equiv \mathcal{F}[n(x)] \equiv \int_{-\infty}^{+\infty} n(x) \exp(-iqx) dx$. This turns the convolutions into multiplications by factors $\gamma_i(q) \equiv \mathcal{F}[g_i(x)] = \exp(-\frac{1}{2}\sigma_i^2 q^2)$. One obtains the spectral dynamics

$$\partial_t \log[s(q)] = -(1 + cN_0^+) - cN_0^+ \gamma_c(q) + b \frac{N_0^+}{\eta + N_0^+} \gamma_b(q) \left\{ 2 - \frac{N_0^+}{\eta + N_0^+} \gamma_m(q) \right\}. \quad (7)$$

Thus, the perturbation components at (character-space) frequencies q decay or grow independently, as $s(q, t) = s(q, 0) \exp(\lambda(q)t)$, with q -dependent eigenvalues $\lambda(q)$ given by the right-hand side of equation (7). Stability of the uniform N_0^+ solution requires $\lambda(q) < 0$ for all q .

The stability question can often be decided simply by truncating terms of $\mathcal{O}(\eta)$ in equation (7), which leaves

$$\lambda(q) = -b + (1-b)\gamma_c(q) + b\gamma_b(q) \{2 - \gamma_m(q)\} + \mathcal{O}(\eta). \quad (8)$$

This approximation suffices in much of parameter space, but there are also interesting regimes where $|\max[\lambda(q)]| = \mathcal{O}(\eta)$. These require the use of the more accurate expression equation (7), with N_0^+ at least up to $\mathcal{O}(\eta^2)$ as in equation (5).

3. STABLE AND UNSTABLE REGIMES

Exact delineation of the regimes in parameter space where N_0^+ is (un)stable can be done by setting equation (7) to zero and solving. It is more interesting, however, to outline the important parameter regimes semi-quantitatively, and analyse some essential features of the various types of instability which can occur.

The analysis becomes particularly simple when the three relevant scales σ_c , σ_b and σ_m differ substantially in relative magnitude, as is often the case. To a first approximation, the behaviour of $\lambda(q)$ (via equation (8), say) may then be understood by observing that each $\gamma_i(q)$ has a characteristic frequency $q \approx Q_i \equiv 1/\sigma_i$ at which it decreases quite steeply from its low- q asymptote $\gamma_i(0) = 1$ to its high- q asymptote $\gamma_i(q \rightarrow \infty) = 0$. Various regimes can then be distinguished on the basis of the relative sizes of the three scales σ_i .

Setting $q = 0$ in equation (8) yields $\lambda(0) = 1 - b$, which is negative in all meaningful cases ($N_0^+ > 0$). Thus, N_0^+ is stable to low- q perturbations. The maximal q for which this remains essentially true is determined by the smallest of the three characteristic frequencies Q_m , Q_b , Q_c , i.e. by the largest of the corresponding scales σ_i . In the opposite limit $q \rightarrow \infty$, one has $\lambda(q) \rightarrow -b$, and this asymptote is essentially reached when q is a few times larger than the largest of the three Q_i . Thus, N_0^+ is also stable to perturbations with wavelengths $L = 2\pi/q$ below the smallest of the scales σ_i .

This stability for very small and very large q is not very surprising. However, inspection of equation (8) shows that $\lambda(q) > 0$ is possible for intermediate q : To maximize λ , all positive terms should still have their $\gamma_i(q) \approx 1$, whereas all negative terms should have their $\gamma_i(q) \approx 0$. This requires a moderately wide q interval $Q_b > q > Q_{i \neq b}$. Indeed, $\max[\lambda(q)]$ approaches its absolute upper bound $\lambda \leq +b$ when $Q_b \gg Q_{i \neq b}$, and the unstable q range can become arbitrarily wide.

Conversely, stability is guaranteed when σ_b is the largest scale in the problem, i.e. when $Q_b \ll Q_{i \neq b}$. Biologically, such a large Mendelian-plus-mutation variance appears to be an unlikely situation. In the rest of this paper, I analyse the more plausible, potentially unstable regimes in some detail.

(a) *Almost indiscriminate mating: σ_m as largest scale*

With σ_m moderately larger than σ_c and σ_b , inspection of equation (8) shows that the system becomes strongly unstable, i.e. the instability is essentially *independent of an Allee effect*, which contributes only $\mathcal{O}(\eta)$ corrections to the approximation, equation (8). It is useful to distinguish between two subregimes which correspond to the relative size of σ_c and σ_b .

The first subregime is $\sigma_m > \sigma_c > \sigma_b$, which may be interpreted biologically as a population of ‘generalists’ with small fecundity range and ditto offspring variance. For sufficiently large σ_c/σ_b , one sees from equation (8) that $\lambda(q)$ can approach its upper bound $\lambda \leq b$ in the q -range $Q_c < q < Q_b$. Very few generations then suffice to let small perturbation components in this q range grow to amplitudes of the same order as N_0^+ . In addition, there can be a $\lambda(q)$ -plateau with $\lambda \approx 1$ at smaller q , namely $Q_m < q < Q_c$. The plateau will be a prominent feature when $\sigma_m \gg \sigma_c > \sigma_b$.

Figure 1. Strong instability for almost indiscriminate mating. Both graphs: mating scale $\sigma_m = 10$ much larger than offspring variation scale $\sigma_b = \frac{1}{10}\sqrt{2}$. Other common parameters: $b = 2$, $c = 1$ and $\eta = 10^{-2}$ (almost irrelevant). Upper graph: ‘moderate generalists’ ($\sigma_c = 1$), i.e. siblings compete directly. Lower curve: ‘specialists’ ($\sigma_c = 1/30$), i.e. siblings hardly compete directly.

An example appears as the upper graph in figure 1. The $\lambda(q)$ -peak (for $Q_c < q < Q_b$) does not yet saturate against the upper bound $\lambda < b$, but it does clearly exceed the level $\lambda \approx 1$ of the plateau for q just below Q_c .

The second subregime is $\sigma_m > \sigma_b > \sigma_c$, which may be interpreted as a continuum of ‘specialists’, with a moderate fecundity range and Mendelian variance. As illustrated in the lower graph in figure 1, the inversion of the smaller two scales removes the previous peak in the $\lambda(q)$ -graph, but leaves a (broad) maximum which reaches roughly the level $\lambda \approx 1$. Again, one can read off this behaviour from equation (8).

(b) *Assortatively mating generalists: σ_c as largest scale*

When σ_c is the largest scale in the problem, there are two subregimes with a possible instability. The first has moderate assortative mating, but a small fecundity range and Mendelian variance, i.e. $\sigma_c > \sigma_m > \sigma_b$. When the three scales are sufficiently separated, $\lambda(q)$ may again approach its upper bound $+b$, as illustrated in the upper graph of figure 2. Thus, an Allee effect is not required for instability, and equation (8) suffices to analyse the situation.

The second potentially unstable subregime is produced by inverting σ_m and σ_b . This describes what may be called ‘xenophobic’ mating, since σ_m is now the smallest of all scales. As illustrated by the lower graph in figure 2, $\max[\lambda(q)]$ now saturates near zero, in accordance with the equation (8) estimate $\max[\lambda(q)] = -\mathcal{O}(\sigma_b^2/\sigma_c^2) + \mathcal{O}(\eta)$ for small σ_b/σ_c . Thus, (in)stability now depends essentially on an Allee effect. One can use equation (7) to obtain the results accurate up to $\mathcal{O}(\eta^2)$.

Without an Allee effect ($\eta = 0$), one has $\lambda(q) < 0$ throughout this subregime. For small σ_b/σ_c , however, one should note that the formally stable continuum $N(x) = N_0^+$ is very sensitive to small perturba-

Figure 2. Strong or weak instability for assortative ‘generalists’. Both graphs: competition scale $\sigma_c = 10$ much larger than any other scale. Other common parameters: $\sigma_b = \frac{1}{10}\sqrt{2}$, $b = 2$, $c = 1$ and $\eta = 10^{-2}$. Upper graph, ‘moderately assortative mating’; $\sigma_m = 1$; lower graph, ‘xenophobic mating’; $\sigma_m = 0.1$.

tions (of $b(x)$, say) which have spectral components in the q -range where $\lambda(q)$ is only negative by a small margin $\mathcal{O}(\sigma_b^2/\sigma_c^2)$. Writing the spectral density of the perturbations as $\nu(q)$, the linear response becomes $s(q) = -\nu(q)/\lambda(q)$, and the ‘gain’ $-1/\lambda(q)$ develops a large ‘resonance’ peak where $\lambda(q)$ almost reaches zero. The response tracks only slow temporal variations: its time constant is $-1/\lambda$. The quasi-periodic array of peaks in $N(x)$ produced by this stable resonance might be hard to distinguish experimentally from one due to a weak instability.

(i) *Species-packing models as limiting cases*

Setting σ_m and σ_b to zero, at finite σ_c , formally reduces equation (4) to classical species-packing models for ($\eta = 0$) clones (e.g. Roughgarden 1979), or ($\eta > 0$) fully speciated sexuals (Hopf & Hopf 1985). However, as suggested by the distinction between the graphs in figure 2, the behaviour of the resulting models depends dramatically on the way in which the two limits $\sigma_m \rightarrow 0$ and $\sigma_b \rightarrow 0$ are taken: a strong (Allee independent) instability occurs roughly if one keeps $\sigma_b < \frac{1}{2}\sigma_m$ while letting both parameters go to zero, whereas one obtains a weak (Allee-dependent) instability when the order of σ_b and σ_m is inverted.

The classical species-packing models are thus structurally unstable, but their ambiguities are resolved by unfolding them to a family of limiting cases of equation (4). Biologically, the simplest modification is to keep σ_v finite, representing (small) mutations. This makes σ_b finite (but much smaller than σ_c), so that one may set $\sigma_m = 0$ without problems. The $\lambda(q)$ graph will then look similar to the lower graph in figure 2, with a wide region $Q_c < q < Q_b$ in which $\max[\lambda(q)] = -\mathcal{O}(\sigma_b^2/\sigma_c^2) + \mathcal{O}(\eta)$. Thus, instability requires an Allee effect, as in the Hopf & Hopf (1985) model. However, the new finite- σ_b model avoids the ‘ultraviolet catastrophe’ (dominant $q \rightarrow \infty$) which occurs in all classical niche-packing models.

(c) *When low-fecundity matings are ‘free’*

In many (but not all) cases of practical interest, the rate of producing (fertile) offspring would not be limited by constraints on mating *per se*, but primarily by the cost of producing and caring for offspring. The model can incorporate such situations, which simply imply a relation between σ_f and σ_m .

For example, consider the extreme case in which unproductive matings are entirely ‘free’, and productive matings all have the same fecundity. Unproductive matings then do not influence the $N(x)$ dynamics, so one may set $f(x) = 1$ and describe the productive mating in equation (2) by means of $g_m(x)$ alone. This implies that $\sigma_f = \frac{1}{2}\sigma_m$ in equation (4). In terms of σ_b , which is what matters in the stability analysis, one gets a constraint $\sigma_m \leq 2\sigma_b$.

This constraint does not affect the ‘xenophobic’ regime $\sigma_c > \sigma_b > \sigma_m$ (lower graph of figure 2). The ‘assortative generalist’ regime $\sigma_c > \sigma_m > \sigma_b$ (upper graph of figure 2), is limited by the constraint, but the Allee-independent instability $\lambda(q) \gg \eta$ survives in most of the remaining part of the regime. The value of $\max[\lambda]$ is reduced, but it remains much greater than η unless the interval $Q_m < q < Q_b$ almost vanishes.

The constraint almost completely removes the strong instabilities found with σ_m as largest scale. The only remaining instability requires σ_v to be relatively small and b to lie in a narrow interval. These extra conditions do not occur with the instabilities found so far, which only require $b > 1 + \mathcal{O}(\eta)$. Taking the ‘specialist’ limit $\sigma_c \rightarrow 0$ of the constrained model, one obtains a model reported in Levin & Segel (1985), which is related to a two trophic level model for which Levin & Segel (1982) performed a full stability analysis.

4. CONCLUSIONS

The results reported here solve the linear stability problem posed by Maynard-Smith & Szathmary (1995). The uniform (‘continuum’) solution N_0^+ is found to be unstable under a large variety of conditions, many of which seem to be biologically realizable. The unstable wavelengths $L = 2\pi/q$ often cover a wide range; one then expects the continuum to break up into structures with little apparent x periodicity.

Strong stability ($\max[\lambda(q)] = -\mathcal{O}(1)$) occurs essentially only if $\sigma_b = \sqrt{\sigma_v^2 + \sigma_f^2}$ is clearly the largest scale. The general constraint $\sigma_f \leq \frac{1}{2}\sigma_m$ then implies that σ_v (Mendelian segregation and mutations) must exceed all other scales, which appears to be a biologically unrealistic regime. In most other cases, the continuum will break up. The quantitative aspects of this instability differ between various regimes, as follows.

Strong instability ($\max[\lambda(q)] = +\mathcal{O}(1)$) occurs in most of the parameter space, e.g. when σ_m is the largest scale, or when σ_b is the smallest scale. The Allee effect is then of no practical importance; the continuum will break up in a few generations.

Weak (in)stabilities ($\max[\lambda(q)] = \mathcal{O}(\eta)$) occur in most of the remaining regime, i.e. essentially for $\sigma_c \gg \sigma_b > \sigma_m$. Now the stability does depend on an Allee-effect:

(1) with an Allee effect $\eta > \epsilon > 0$, where $\epsilon = \mathcal{O}(\sigma_b^2/\sigma_c^2)$, a true (Turing-type) instability occurs, but it will take $\mathcal{O}(1/\eta)$ generations for the continuum to break up;

(2) with no Allee effect (or $\eta < \epsilon$), the system is formally stable, but only by a margin of ϵ (in a certain q -range). ‘Resonant’ amplification of small (quasi-)static perturbations then produces roughly x -periodic peaks in $N(x)$.

In addition, classical niche-packing models are recovered as a family of limiting cases, and this helps to understand some peculiarities of the older models. The present model also appears to provide a good framework for extending the analysis to questions of invasibility, and to an analysis of the highly nonlinear behaviour of sharply peaked quasi-species, which are expected to emerge when the $N(x)$ modulations produced by the linear instabilities studied here reach amplitudes similar to the uniform solution level N_0^+ . Simulations (to be reported elsewhere) confirm that narrow (but finite-width) peaks are indeed produced

almost invariably when the uniform continuum is linearly unstable.

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