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Intraspecific resource competition as a cause of sympatric speciation

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Rosenzweig (1978), Bengtsson (1979), and Gibbons (1979) argue that intraspecific resource competition might cause sympatric speciation. Bengtsson emphasizes that the environment need not be spatially or temporally heterogeneous in any way.

> [In most models of speciation], the fitness value of an animal is determined by the genotype it has, and the habitat in which it lives. In a more realistic model it should also depend on how much necessary resource is available for the animal and the competition from other genotypes for this resource.
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> Models can be constructed which take into account such competition between genotypes. In a special case one can find the exact conditions for the stable coexistence of two incipient species, which have some degree of gene flow between them but also slightly different resource utilization distributions.
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> An interesting property of this class of models is that they show how sympatric speciation can occur in a species where all animals live in the same habitat and under the same fitness regime, but differ, due to their genetic constitution, in their resource utilization.

Here I elaborate this proposal and describe a simple genetic model in which intraspecific resource competition leads to speciation. In the discussion, I point out that models of this kind are more closely related than they may at first appear to be, to some previously studied models of sympatric speciation.

Phenotype-dependent resource competition

Consider a species in which individuals differ with respect to a trait that enables them to exploit different regions of a resource spectrum. To fix ideas, think of a quantitative character (say, beak size) that tends to scale with overall body size, and let the corresponding resource be a food (say, seeds) that occurs in a more or less continuous distribution of sizes. For the sake of simplicity, suppose that each individual will consume only those food items that fall within a well-defined range of sizes, the particular range being determined by the individual's phenotype. Thus individuals with

large beaks tend to be large and to take large seeds, while those with small beaks tend to be small and to take small seeds. Given these assumptions, it follows almost inevitably that individuals of a given size will stand more directly in competition with each other than they will with individuals of sizes different from their own. Other things being equal, the expected fitness of the members of a given size class will be negatively frequency-dependent if there is any competition for seeds.

Let beak size be influenced by genes at many polymorphic loci and also by environmental variation. Then if the species mates randomly, there will be an approximately normal distribution of beak sizes. If the distribution of available seed sizes is also normal (after any necessary corrections for allometry), then the population can easily evolve to an equilibrium distribution of gene frequencies such that the resulting distribution of beak sizes 'matches' the distribution of seed sizes. At this equilibrium all phenotypes (and therefore all genotypes) have equal expected fitnesses (Slatkin, 1979).

But what happens if the distribution of available seed sizes is *not* normal? For example, suppose that over the range of seed sizes used by the species the distribution is uniform. Then individuals in the tails of the beak-size distribution will enjoy higher fitnesses than will those in the centre, and the species will be subject to disruptive selection on beak size. Given our assumptions of polygenic control, moderate heritability, random mating, and phenotype-dependent resource utilization, there is no way the species can exhibit a distribution of phenotypes that matches a uniform or other non-normal distribution of available resources.

How might a better match be realized between the distributions of phenotype and of resource? Each of the assumptions just mentioned suggests a different way in which this might be done. For example, the development of beak size could be uncoupled from direct genotypic control, such that a rectangular distribution of beak sizes resulted. Or the preferences of individuals of a given size for seeds of a given size might somehow be modified. In principle, each of these scenarios is equally plausible. But it is easy to imagine constraints of various kinds (mechanical, developmental, or merely phylogenetic) that could prevent such changes from occurring, at least to the extent needed to bring about a good fit between the distribution of phenotypes and that of resources.

The remaining possibility is that panmixia might give way to a system of positively assortative mating. This would flatten the distribution of phenotypes, without requiring that the genetics or development of the trait be modified in any way. It seems intuitively clear that assortative mating could be favoured under these conditions. Compared with parents who mated randomly, those who mated assortatively would have a greater number of offspring with extreme (and therefore relatively fit) phenotypes.

This intuition is supported by the many explicit models in which assortative mating evolves under regimes of disruptive selection (e.g. Maynard Smith, 1966; Dickinson & Antonovics, 1973; Udovic, 1980; Felsenstein, 1981). I have used a simple deterministic simulation to study the conditions under which different schemes of assortative mating may lead to speciation, under the assumptions discussed above.

Assortative mating with resource competition

All versions of the model share the following features. The species is haploid and has a resource-utilization phenotype that is influenced by two independently segregating loci, A and B. Alleles A_1 and B_1 each contribute a genotypic value of '1', and alleles A_2 and B_2 each contribute '2'. Thus the four haploid genotypes map onto three (two-locus) genotypic values. But genotypic values do not absolutely determine phenotypic values. There is assumed to be a substantial and unavoidable component of environmental variation, such that each genotypic value gives rise to a phenotypic value immediately below or above itself with probability $\frac{1}{4}$. Thus there are five distinct phenotypic values, and the four genotypes give rise to them according to the following scheme.

		Phenotypic values				
Genotype	Genotypic value	1	2	3	4	5
A_1B_1	2	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$		
A_1B_2	3		$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	
A_2B_1	3		$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	
A_2B_2	4			$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$

The phenotypic values correspond to intervals along the resource axis. Individuals of phenotype '1' take *only* resources of type '1' (e.g. small birds take small seeds), and so on for the other phenotypes and resource classes. Thus direct resource competition takes place only between members of a given phenotype class, but three or even all four of the genotypes may be present within a given phenotype class.

All members of a phenotype class have the same expected fitness, which is directly proportional to the resource abundance, and inversely proportional to the number of individuals competing for that resource. Letting i index phenotype and resource classes, $W_i = R_i/F_i$, where W is fitness, R is resource density, and F is population density. Thus the summed fitness of

all of the members of phenotype class i must be equal to R_i. Individual fitnesses are treated formally as viabilities (that is, as probabilities of entering the mating pool), but they could just as well be thought of as relative fecundities (for females) and as relative probabilities of mating, given a particular pattern of female choice (for males).

Generations are discrete and non-overlapping. After selection, mating takes place in a single large pool. The implicit primary sex ratio is 1:1, and there are no sex differences in viability, so male and female genotype frequencies are always equal. In some versions of the model there is a locus governing female choice, with alleles C_1 (choosing) and C_2 (random mating). Females carrying the C_1 allele select mates according to one or another of the schemes described below. The A, B, and C loci are all unlinked. In some versions of the model there is another unlinked locus (D) that determines an arbitrary, selectively neutral phenotypic marker.

A fully deterministic algorithm was used to advance the population from one generation to the next, according to the rules and assumptions outlined above. This algorithm is equivalent to a system of recurrence equations in the genotype frequencies.

Four different resource distributions were employed, as set out in the following table.

	Class				
Distribution	1	2	3	4	5
Binomial	0.0625	0.25	0.375	0.25	0.0625
Uniform	0.2	0.2	0.2	0.2	0.2
Overdispersed	0.075	0.25	0.35	0.25	0.075
Underdispersed	0.05	0.25	0.4	0.25	0.05

Note that all four distributions are symmetrical. Thus the equilibrium gene frequencies at the A and B loci are equal to $\frac{1}{2}$, at least under random mating. The 'binomial' resource distribution is the null case, corresponding to the phenotype distribution that occurs under random mating. The 'uniform' distribution is extremely overdispersed. The 'overdispersed' and 'underdispersed' distributions are only mildly so, relative to the binomial distribution.

Five different schemes of female choice were considered. These schemes are described below, together with the results. A summary is given in Table 1.

(1) *Genotypic assortative mating (A and B loci).* Under this scheme of mating, a C_1 female mates only with males whose genotypes at the A and B loci are identical to her own. For example, a female of genotype $A_1B_2C_1$ will

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Table 1. *Results of five schemes of female choice under three distributions of resource*

Basis of assortative mating	Resource distribution		
	Binomial	Overdispersed (incl. uniform)	Underdispersed
(1) Genotype (A/B) Choice polymorphic	Choice is neutral	Choice is favoured and speciation occurs	Choice is favoured and speciation occurs
(2) Phenotype (A/B) Choice polymorphic	Choice is eliminated	Choice is favoured but speciation does not occur	Choice is eliminated
(3) Phenotype (A/B) and markers (D) Choice fixed	Choice would not be favoured	Character-displaced species of equal abundance form around the two markers	Choice would not be favoured
(4) Markers (D) Choice fixed	Markers are neutral, do not change in frequency	Character-displaced species of equal abundance form around the two markers	A low-variance species (mainly A_1B_2 or A_2B_1) forms around one marker, and a high-variance species (all A/B genotypes) forms around the other
(5) Markers (D) Choice polymorphic	Not considered	Choice is favoured only very weakly until it is at high frequency; then character-displaced species form, as above	Not considered

mate either with $A_1B_2C_1$ or with $A_1B_2C_2$, the relative frequencies of the two possible matings being equal to the relative frequencies of the two kinds of acceptable males. This is a highly artificial system of choice, because it allows females to distinguish between male genotypes that express the same phenotypic value. In the case of A_1B_2 and A_2B_1, females can even choose between genotypes with the same genotypic value.

Under *any* resource distribution other than the null (binomial) distribution, the choice gene (C_1) goes quickly to fixation. At fixation for C_1 there are four 'species', each of which is genetically homogeneous at the A and B loci. Choice is neutral under the binomial resource distribution because a binomial distribution of phenotypes can be maintained with any amount of assortative mating, when the frequencies of A_1 and B_1 are equal to $\frac{1}{2}$.

(2) *Phenotypic assortative mating* (*A and B loci*). Under this scheme of mating, females can distinguish only between the phenotypes of potential mates, not between genotypes or even genotypic values. (Of course, males of phenotypes '1' and '5' must be A_1B_1 and A_2B_2, respectively.) The choice gene is eliminated under the binomial and underdispersed resource distributions, because phenotypic choice inevitably flattens the phenotype distribution (as genotypic choice does not). If the resource distribution is highly overdispersed (uniform), then the choice gene goes quickly to fixation. But speciation does not occur, because all possible matings continue to take place at appreciable frequencies. (Note that all four A–B genotypes are present in the central phenotypic class.) Speciation could occur under this resource distribution and scheme of choice only if there were no environmentally induced phenotypic variation.

The mildly overdispersed resource distribution would be matched exactly with A-locus and B-locus gene frequencies of $\frac{1}{2}$, and a moderate amount of assortative mating. Thus, under this distribution, the two alleles at the choice locus are expected to find a stable interior equilibrium. They do, but the equilibrium frequency of C_1 (the choice allele) is *higher* than expected, giving rise to an equilibrium phenotype distribution (0.076, 0.25, 0.348, 0.25, 0.076) that is even flatter than the resource distribution.

Why is there *more* assortative mating at equilibrium than is needed to equalize individual fitnesses? The reason seems to be that female choice creates a weak inclusive fitness effect (Hamilton, 1964). At equilibrium, the frequency of C_1 is 0.645 in the terminal phenotypic classes (1 and 5), 0.620 in the subterminal classes (2 and 4), and 0.609 in the central class (3). Thus members of the same phenotype class are positively related at the C locus. On average, a female who chooses will thereby increase the reproductive success of a male who is more likely to be carrying the C_1 allele than is a male taken at random from the population. The coefficient of relatedness (Michod & Hamilton, 1980; Seger, 1981) is very small ($R \simeq 0.0004$), but so is

the expected reduction of fitness in the offspring produced by assortative matings.

This is not an instance of runaway selection (Fisher, 1930; O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982), at least not in the usual sense, because the *average* female preference is for an *average* male phenotype. Perhaps it could be viewed as a case of simultaneous runaway selection in opposite directions. In any event, it suggests that directional runaway selection might usefully be analysed in terms of inclusive fitness effects at the choice locus (or loci).

(3) *Phenotypic assortative mating (A and B loci) with genotypic assortative mating (D locus).* Under this scheme the population is assumed to be fixed for allele C_1, so that all females are mating assortatively with respect to phenotypes, as described under scheme (2), above. This assumption is logical only if the resource distribution is overdispersed, because only in that case would choice be favoured. The C_1 allele is now assumed to confer on its bearers a *generalized* preference for mates that resemble them in any detectable way. Alleles D_1 and D_2 are introduced, controlling some completely arbitrary, selectively neutral, visible phenotypic difference (say, bright versus dull plastic leg bands). Thus females mate only with males whose functional phenotypes *and* marker phenotypes are the same as their own.

If the D alleles are introduced at a low level of phase disequilibrium with the alleles at A and B, the initial phase disequilibria grow rapidly, and the frequencies of D_1 and D_2 converge on $\frac{1}{2}$. Depending on the signs and relative magnitudes of the initial phase disequilibria, A_1 and B_1 are drawn into association with one of the D alleles, while A_2 and B_2 are drawn into association with the other D allele. Under the uniform resource distribution this process goes to completion, leaving in the end only two genotypes, $A_1B_1D_i$ and $A_2B_2D_j$, at equal frequencies.

It is of no interest that 'speciation' takes place under this scheme. The assumption that females will mate assortatively with respect to a number of different traits (including the arbitrary markers) means that from the beginning the markers necessarily define two reproductively isolated mating pools. The interesting result is that, as expected (Slatkin, 1980), these mating pools become genetically and phenotypically differentiated.

(4) *Genotypic assortative mating (D locus).* This scheme is the same as scheme (3), above, except that females choose *only* with respect to the arbitrary marker, not with respect to the functional phenotypes of their potential mates. As with the previous scheme, two character-displaced species form around the two markers if the resource distribution is overdispersed. Under the null (binomial) resource distribution the markers are neutral, because choice with respect to an arbitrary marker *need not*

lead to phenotypic assortment and *does not* do so unless such assortment is favoured for other reasons.

A strange pattern of association builds up if the resource distribution is underdispersed. A low-variance species consisting mainly of A_1B_2 or A_2B_1 forms around one of the markers, and a high-variance species consisting of all four genotypes forms around the other. The two species have nearly identical average phenotypes, so they are not character-displaced in the usual sense. Instead, the low-variance species specializes on the centre of the resource distribution while the high-variance species specializes on the tails. Given the highly artificial genetic constraints built into the model, this is the most efficient way to divide the resource distribution. Presumably the high-variance species would itself speciate into a small (A_1B_1) and a large (A_2B_2) species, each one exploiting a single tail of the resource distribution, if another phenotypic marker were introduced.

(5) *Genotypic assortative mating* (*C and D loci*). This final mating scheme involves all four loci. It is just like scheme (4) above, except that the population is *not* initially fixed for the choice gene. Only those females who actually carry allele C_1 choose mates who are like them at the D locus. The rest mate randomly with all of the available males.

Will choice itself be favoured, under an overdispersed resource distribution? The outcomes of schemes (1) and (2) clearly suggest that it should be, if D_1 and D_2 become associated with A_1B_1 and A_2B_2 (thereby signalling the presence of low and of high genotypic values). And the outcome of scheme (4) suggests that choice will tighten these very associations. Thus the entire process ought to lift itself up by its own bootstraps.

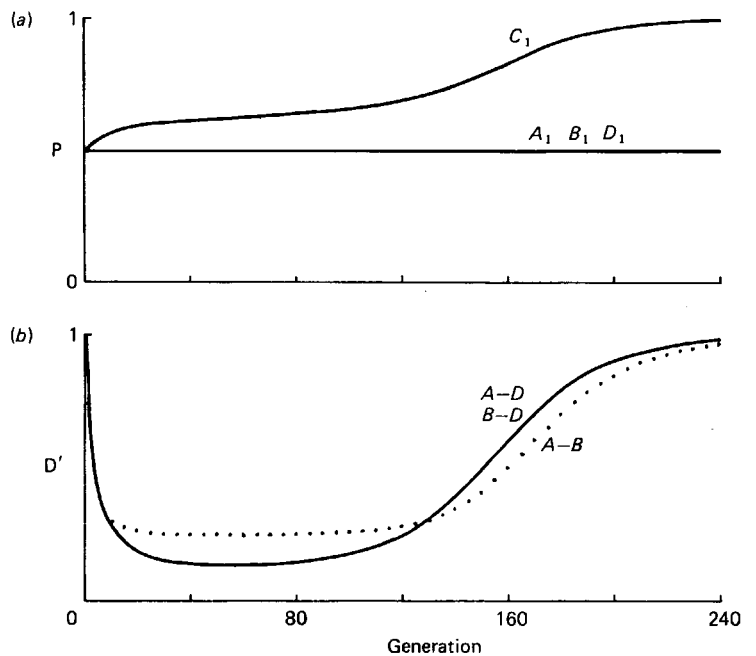
Unfortunately, this does not usually happen. In all of the cases studied the resource distribution was made uniform, providing very strong selection in favour of assortative mating. All runs were started with gene frequencies of $\frac{1}{2}$ at loci A, B and D, and with the largest possible degree of phase disequilibrium (all $A_1B_1D_1$ and $A_2B_2D_2$). If C_1 is introduced at a frequency of 0.25, it quickly rises to a frequency of 0.28, but then its progress comes to a virtual halt as the disequilibria between D and A–B decay to very small values. (Selection in favour of extreme phenotypes maintains the phase disequilibrium between A and B at a moderately high level.) If C_1 is introduced at a frequency of 0.5 it goes to effective fixation within 240 generations, but it does so by the dynamically strange route illustrated in Fig. 1. There is a sharp rise (generations 1–20) owing to the initial, artificially high phase disequilibria. Then there is a long plateau (generations 20–100) during which the frequency of C_1 very slowly increases while the phase disequilibria hold fairly steady at moderate values. Then there is a second, accelerating rise to fixation (generations 100–240), during which the phase disequilibria increase. At the end there is complete disequilibrium and speciation.

Although a strong positive feedback between choice and the conditions favouring choice does appear during this final period, it seems to require that the choice gene already be at high frequency, and it therefore fails to explain how choice with respect to an arbitrary marker could spread (at least at an appreciable rate) when rare.

Discussion

Taken together, the models described here clearly support Bengtsson's claim that 'sympatric speciation can occur in a species where all animals live in the same habitat and under the same fitness regime, but differ, due to their genetic constitution, in their resource utilization'. It should be stressed that speciation occurs not merely because individuals *differ* genetically in their resource utilization, but also, and in particular, because there are *constraints* on the possible *distributions* of their phenotypic differences.

Fig. 1. Gene-frequency and phase disequilibrium trajectories in the four-locus model (scheme 5). The illustrated run was started with equal frequencies of genotypes $A_1B_1C_1D_1$, $A_1B_1C_2D_1$, $A_2B_2C_1D_2$, and $A_2B_2C_2D_2$. (*a*) Gene frequencies. The choice gene (C_1) goes to fixation, as described in the text. (*b*) Standardized pairwise phase disequilibria for loci *A*–*B* (dotted line), and for loci *A*–*D* and *B*–*D* (solid line). The phase disequilibria decay to intermediate values from their initially maximal values, and then increase to maximal values as the choice gene goes to fixation and speciation occurs.



These constraints arise from fundamental properties of the species' genetic and developmental systems. In the context of the models these properties are taken to be unalterable, but in reality it would be necessary only that the genetic and developmental constraints be less readily alterable than the mating system. Thus the models suggest that sympatric speciation could provide, figuratively speaking, an easy way out of a difficult ecological and developmental bind.

But if there is environmentally induced variation of the functional phenotype so that genotypes cannot be distinguished unambiguously, then speciation will not occur unless mating is assortative with respect to some other, genetically unambiguous phenotypic difference, one that can be used as a proxy for the functional genotypes that are under disruptive selection. The four-locus model (scheme 5) suggests that such a system will not necessarily evolve spontaneously, even though it would be advantageous and stable once evolved. This would seem to pose a serious difficulty for this mechanism of sympatric speciation, unless *generalized* systems of female preference (along the lines of scheme 3) tend to evolve, preadapting the species for incorporation of an arbitrary marker into its system of assortative mating.

Many recent models of sympatric speciation trace back directly to Maynard Smith's (1966) development of Levene's (1953) model. The model developed here is no exception. It is, in fact, a Levene model with habitat selection (the process Maynard Smith considered most likely to cause speciation). But the form of habitat selection is peculiar in two respects. First, it is only *partial* habitat selection, because there is unavoidable environmental variation of the phenotype. Second, individuals 'return' to the different 'habitats' (= resource classes) in proportions that are not free to evolve independently. The genetic system constrains the phenotypes to occur in proportions that will, in general, *not* match the carrying capacities of the habitats, even if there is perfect assortative mating within habitats (as in scheme 2, phenotypic assortative mating). In most Levene models, positively assortative mating evolves because different phenotypes can specialize on qualitative differences between the habitats. In this one the phenotypes are already fully specialized, to the point of being *limited* to different 'habitats'. Assortative mating evolves because the frequency distribution of 'habitats' does not match that of phenotypes, if mating occurs at random.

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