



Department of Mathematics

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To whom it may concern

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**Report: Master's Thesis by Pavel Payne**

The title of Pavel's master's thesis is "The role of genetic variance in speciation". Speciation is here understood as sympatric speciation, that is, speciation in the absence of a barrier to gene flow. It is widely accepted that negative frequency-dependent disruptive selection is then a necessary requirement for speciation. Under such a selective regime speciation may occur according to the following scenario. First genetic variation builds up and can be maintained in a protected genetic polymorphism by negative frequency-dependent selection. Disruptive selection means that extreme phenotypes are favored over intermediate ones. Under most genetic architectures, if disruptive selection acts on a one-dimensional quantitative trait, heterozygotes will have lower fitness than homozygotes. In this case, any mechanism that prevents the formation of heterozygotes is selectively favored. In particular, the evolution of assortative mating has received much attention and can indeed lead to the completion of the speciation process.

Pavel's master's thesis focuses on the first step in this scenario: the maintenance of genetic variation in a protected polymorphism. He investigates the possibility to maintain genetic variation under negative frequency-dependent disruptive selection based on a two-patch Levene-model, a mayor workhorses of theoretical speciation research. In the beginning of his thesis Pavel points out that most work based on the Levene-model assumes a highly symmetric structure, in particular, equal patch sizes. The reason for this frequent assumption is clear: it greatly facilitates an analytical treatment of the model. On the downside, the possible effect of symmetry on the parameter range allowing for the maintenance of genetic variation might have been underestimated. This is the focus of Pavel's work.

Pavel uses a haploid version of the Levene-model with either two or three bi-allelic loci. He then investigates the potential for the maintenance of genetic variation as a function of (1) the strength of within-patch viability selection, measured by the selection coefficient  $s$  that is subtracted from 1 for each deleterious allele, (2) the degree of epistasis between two or more deleterious alleles, (3) the degree of asymmetry in the contribution of the two patches to a common dispersal pool, (4) the amount of recombination between loci and (5) the degree of asymmetry in the patch specific strength of selection.

The general finding of the thesis is that strong epistatic effects, leading to convex trade-offs, high recombination rates and weak selection all narrow down the parameter region where genetic variation can be maintained. Here the potential to maintain genetic variation is expressed as the range of niche proportions where the boundary equilibria are unstable. The more adverse the conditions for genetic polymorphism, the higher the degree of symmetry that is required to maintain genetic polymorphism.

Based on these findings Pavel concludes that the standard scenario of sympatric speciation becomes rather implausible. The reason is that generally systems would have to be highly symmetric in order to maintain the genetic variance that is the starting point of the speciation process. In my opinion Pavel raises a potentially important point that might have been under-appreciated in the past. In conclusion, I recommend to accept the thesis of Pavel Payne.

However, I believe that the conclusion that ecological sympatric speciation becomes very unlikely is premature as I will detail in the questions that I would like to ask the candidate:

1. Whether sympatric speciation is likely or not depends on its definition. If the term is used as in the 2004-book by Sergey Gavrilets, that is, as speciation where mating is independent of the place of birth, it is indeed very difficult for reasons other than those raised in this thesis. However, researches in speciation seem to increasingly agree that most speciation events do neither occur in complete sympatry nor in complete allopatry. Instead, most speciation probably occurs in the face of limited gene flow which might even fluctuate over time, that is, in parapatry. This scenario is not discussed by Pavel and I would like him to speculate how his results change if the migration rate in his model is decreased from  $m = 1/2$ .
2. I would like to raise the possibility that the result presented in figure 8 are erroneous, at least, I find them counter-intuitive. In this figure Pavel reports his findings for the case that selection is asymmetric in the two patches. More specifically, the figure shows the range of niche proportions that allow for the maintenance of genetic polymorphism as a function of  $s_1$  and  $s_2$ , the selection coefficients of deleterious alleles in the two patches. The range of niche proportions is expressed as  $|\Delta c|$ , which according to my understanding equals  $|c_1 - c_2|$ , i.e., the difference in niche proportions where polymorphism is maintained. Intuitively, I would think that if  $s_1 \neq s_2$ , i.e., if selection is asymmetric, then the possibility to coexist depends on whether  $c_1 > c_2$  or  $c_1 < c_2$ . In other words, my expectation is that the possibility for coexistence depends on  $c_1 - c_2$  and not on  $|c_1 - c_2|$ . More precisely, if  $s_1 > s_2$ , i.e., if selection against alleles  $A$  and  $B$  in patch 1 is stronger than selection against alleles  $a$  and  $b$  in patch 2, then coexistence should be easier if patch 2 is less productive than patch 1 (i.e.,  $c_1 < c_2$ ). This would make it more difficult for the superior alleles  $a$  and  $b$  to swamp the population. I would like to ask the candidate for clarification.

(Claus Rueffler)