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''ADAPTIVE SPECIATION''—IT IS NOT THAT EASY: A REPLY TO DOEBELI ET AL.

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The picture of the world of speciation according to Doebeli et al. (2005) is very romantic. There are the innocent, oppressed victims: ''evolutionary biology'' in general and ''speciation research'' in particular. There are the shady villains: ''past dogma,'' ''old geographic classification of speciation,'' and ''traditional population genetic approaches'' as well as their ''adherents'' (Mayr, Dobzhansky, and others including the author of this response). There are also the brave, young revolutionaries: theories of ''adaptive dynamics'' and ''adaptive speciation'' that finally bring freedom to the masses of biologists after decades of the ''shackles of allopatry.''

Here I suggest that this is not an accurate picture of reality and comment on the claims that adaptive speciation is theoretically plausible and that sympatric speciation is all but inevitable. A few clarifications are in order. (1) I gladly admit that research on ''adaptive dynamics'' has significantly improved our understanding of how genetic variation can be maintained under disruptive frequency-dependent selection. I also believe that work on ''adaptive speciation'' has been very stimulating for the field of speciation in general. (2) I do not think I really have a stake in the old arguments on allopatric versus parapatric versus sympatric speciation. In my work, I have studied models of all these processes. In fact, as a theoretician I am probably biased towards sympatric speciation rather than against it. Indeed, my work has already lead to analytical results on the conditions for sympatric speciation in eleven different models, both classical and new (e.g., Gavrilets 2004). I am puzzled how my Perspective article (Gavrilets 2003) can be viewed as a defense of ''allopatric dogma'' given that it devotes four pages to demonstrating how sympatric speciation can occur in mathematical models. (3) The clearly stated goal of my article was to give a sample of speciation models for which analytical progress has been possible, which meant that a great deal of numerical papers, including those published under the umbrella of ''adaptive dynamics'' or ''adaptive speciation,'' were not discussed. Models of reinforcement were not discussed for exactly the same reason. The potentially promising analytical approaches being developed by Kirkpatrick and Servedio (e.g., Servedio and Kirkpatrick 1997; Kirkpatrick and Servedio 1999; Kirkpatrick 2000; Servedio 2000) assume weak selection and, thus, in my opinion, currently do not allow us to evaluate the real theoretical significance of reinforcement (because weak selection will only result in weak effects). The analytical results on ''adaptive dynamics'' cited by Doebeli et al. (2005) are concerned with the maintenance of genetic variation in asexual populations rather than with the evolution of reproductive isolation and speciation. For those interested in more details on numerical models, Gavrilets (2004) reviews general theoretical speciation research, and Waxman and Gavrilets (2005) provide a critical review of adaptive dynamics. (4) I agree that extensive numerical simulations can indeed provide a good understanding of a mathematical model. The problem is that theoreticians often do not perform extensive simulations. Moreover in many situations, particularly if there are more than five or six parameters, extensive numerical simulations are simply not feasible.

Before discussing the plausibility of ''adaptive speciation,'' it is necessary to clarify the meaning of this term. One straightforward interpretation is that this is a speciation process in which genetic changes underlying divergence and reproductive isolation are driven by selection (as opposed to changes driven by mutation and random genetic drift). This is however not how Doebeli et al. define adaptive speciation. What they mean by adaptive speciation is a much narrower category of ''speciation processes in which the splitting is an adaptive response to disruptive selection caused by frequency-dependent biological interactions'' (Dieckmann et al. 2004, p.4). ''Adaptive speciation'' requires ecological contact. This implies that allopatric speciation cannot be ''adaptive.'' Another crucial feature of ''adaptive speciation'' is that its driving force is frequency-dependent rather than constant selection. This implies that speciation driven by adaptation to discrete ecological niches is not ''adaptive speciation'' according to Doebeli et al. In particular, if two races of a phytophagous insect speciate via adaptation to two different host plants (e.g., Bush 1969; Feder 1998; Berlocher and Feder 2002) or two different fish morphs adapt to benthic and limnetic environments (e.g., Schluter 2000) or a number of different lizard ecomorphs adapt to different parts of trees on a Caribbean island (e.g., Losos 1998; Losos et al. 1998) or Hawaiian spiders adapt to different ecological niches (e.g., Gillespie 2004) it is not ''adaptive speciation.'' Unfortunately, Doebeli et al. (2005) fail to provide biological examples of ''adaptive speciation.'' I suggest that the disparity between a narrow focus of adaptive speciation à la Dieckmann et al. (2004) and Doebeli et al. (2005) and a much broader interpretation of this term will probably result in a lot of confusion.

From a theoretical point of view ''adaptive speciation'' can potentially occur both in sympatric and parapatric geographic settings. However because most of the new ''revolutionary'' claims have so far focused on sympatric speciation, I will concentrate on this geographic mode, in general, and on sympatric speciation driven by frequency-dependent selection, in particular.

A general conclusion that emerged from several decades of theoretical work is that although sympatric speciation is theoretically possible, conditions are rather specific. However, this conclusion is now declared to be flawed by a group of theoreticians forcefully promoting in a concerted way ''adaptive dynamics'' and ''adaptive speciation.'' The new view being advocated is that sympatric speciation occurs easily. Why are the previous conclusions so different from the new ones? The answer according to Doebeli et al. (2005) is that old models used ''rather simple genetic and ecological assumptions'' whereas new models using ''more realistic genetic assumptions than were used earlier on'' clearly show that sympatric speciation is a very plausible process.

The most cited paper in support of this claim is that by Dieckmann and Doebeli (1999). What are the ''more realistic genetic assumptions'' of Dieckmann and Doebeli? It is hardly their assumption that assortative mating is extremely strong but that the costs of being choosy are completely absent. In fact, there are multiple costs of choice reducing female viability, mating success, and fertility (e.g., Jennions and Petrie 1997; Pomiankowski 1987) and these costs will tend to reduce choosiness. Clearly, it is also not their assumption that mutation rates are two to three orders of magnitude higher than realistic values. Neither is it their setting initial conditions in numerical simulations in such a way that the population has the maximum amount of genetic variation at the loci controlling nonrandom mating. According to the authors more realistic assumptions are (1) allowing for a larger number of loci, and (2) allowing for random genetic drift.

Twenty or thirty years ago performing numerical simulations with a large number of loci was indeed very difficult and almost never attempted (but see Crosby 1970). Taking numerical simulations to a new level of complexity is an undeniable achievement of modern theoreticians. However, there is a problem with the interpretations of Doebeli et al. (2005). As common knowledge already has it (e.g., Mayr 1947) and as is apparent from the numerical results of Dieckmann and Doebeli (1999), increasing the number of loci actually makes sympatric speciation more difficult rather than easier. The reason is simple: with more loci each individual allele experiences weaker selection, and simultaneously recombination becomes more powerful in destroying linkage disequilibrium being created by selection. Therefore the increased realism of numerical models with regard to the number of loci has nothing to do with showing the plausibility of sympatric speciation. As for random genetic drift, one of its general effects is to reduce genetic variation and, thus, make within-population genetic divergence more difficult. In the simulations of Dieckmann and Doebeli (1999), as well as in many other numerical models of sympatric speciation, this effect of random genetic drift is not apparent because the authors choose unrealistically high mutation rates and set initial genetic variation at the highest possible level (with all alleles at frequency 0.5). In a sense, making these assumptions moves the population much closer to a set of states from which speciation can occur rapidly than it would be under more natural initial conditions. As a result, the population does not evolve higher levels of assortativeness in mating but rather sorts the huge pre-existing variation. The two relevant and obvious questions are (1) by what biological mechanism(s) did this variation come to exist, and (2) what happens if initial genetic variation is set at a low level (e.g., at a mutation-selection balance state with random mating). The published work on ''adaptive speciation'' provides no answer to these questions. Probably with a certain creativity a satisfying answer to the first question can be discovered (it would be interesting to know it). The second question is considered below.

Why does sympatric speciation occur so easily in Dieckmann and Doebeli (1999) models? To understand this one needs to look at their models more closely. They consider two classes of models. In the first class, both viability and mating preferences are controlled by the same quantitative character. This is a ''magic trait'' model in the terminology of Gavrilets (2004). That sympatric speciation can happen in this type of model was established a long time ago (e.g., Moore 1981; Slatkin 1982; Kondrashov 1983a,b, 1986; Rice 1984). This theoretical conclusion has also received strong experimental support (Rice 1985; Rice and Salt 1988, 1990). What is required for speciation in ''magic trait'' models is sufficiently strong disruptive selection and sufficiently strong positive assortative mating. Recombination which potentially can be very effective in constraining sympatric speciation (e.g., Felsenstein 1981) is largely irrelevant in this scenario. A new and important elaboration of this model due to Dieckmann and Doebeli (1999) is the addition of a quantitative trait controlling the degree of assortativeness. Previously, speciation models allowed for only a single modifier locus (e.g., Balkau and Feldman 1973; Endler 1977; Sawyer and Hartl 1981; Sanderson 1989). The goal of Dieckmann and Doebeli (1999) was to show that assortativeness can gradually strengthen via a second-order selection against low-fitness intermediate genotypes. The authors observed sympatric speciation on the time scale of a few hundred generations which, in their view, warranted the claim that sympatric speciation ''occurs easily.'' However because they have chosen inappropriate initial conditions and parameter values and neglected costs of being choosy this claim is not justified. In an analogous but much simpler one-locus model, Matessi et al. (2001) showed that unless competition is very strong, the population evolves to a state where the degree of assortativeness is genetically variable and is maintained at an intermediate level rather than going to extremely high levels. Similar behavior is expected in multilocus models. Recently Bolnick (2004); Kirkpatrick and Nuismer (2004) and Gourbiere (2004), using multilocus models, showed that incorporating even weak costs of being choosy and making assortative mating weaker significantly reduces the probability of sympatric speciation. Similar effects are observed if mutation rates are set at biologically realistic values and initial genetic variation is reduced to that at a mutation-selection balance (S. Gavrilets, unpubl. data). Therefore, although ''magic trait'' models provide the easiest way to achieve sympatric speciation (Gavrilets 2004), even in these models speciation occurs only under certain conditions which hardly can be interpreted as ''broad.''

The second class of models studied by Dieckmann and Doebeli (1999) considers a much more general and much less theoretically explored case, in which mating preferences are controlled by a trait different from the one underlying viability. Now sympatric speciation requires the establishment of strong linkage disequilibria between the loci controlling these two traits. In Dieckmann and Doebeli's simulations, which were subject to the same limitations as discussed above, sympatric speciation was observed on the time scale of few hundred to twenty thousand generations. To understand the mechanism of speciation in these simulations it is helpful to start with the classical Udovic (1980) model. In this model, each of the two traits is controlled by a single diallelic locus, both loci are unlinked, the strength of assortative mating is fixed, and the effects of genetic drift are disregarded. In the Udovic model, sympatric speciation occurs if $s + a > 1$, where s is the relative fitness loss of heterozygotes at the viability locus and a is the probability of assortative mating (Gavrilets 2003, 2004). Let us generalize the Udovic model by introducing an additional multiallelic locus controlling a, allow for mutation, and consider a finite population. The dynamics of allele frequencies at the third locus will be largely driven by mutation and random drift. (Although higher levels of assortativeness will be advantageous if disruptive selection is sufficiently strong, the selection for increased a induced by this effect is very weak, i.e., second order; e.g., Crosby 1970). Starting with a close to 0 (i.e., with random mating), the value of a will eventually drift stochastically towards high values that make the condition $s + a > 1$ satisfied. Once this happens, sympatric speciation will follow rapidly. Note that the time scale for speciation will be largely controlled by the interactions of mutation and genetic drift at the modifier locus. Although in this three-trait model, each trait is controlled by a single locus rather than by multiple loci, the general mechanism of sympatric speciation appears to be the same as in Dieckmann and Doebeli (1999). It should be immediately obvious that starting with low levels of genetic variation, realistically low mutation rates, increasing the number of loci, introducing costs of being choosy, or increasing the population size will all act against sympatric speciation. These expectations are supported by numerical simulations of the Dieckmann and Doebeli model (S. Gavrilets, unpubl. data). All this implies once again that conditions for sympatric speciation are not ''broad'' at all.

My overall reading of Dieckmann and Doebeli (1999) is that they show the possibility of sympatric speciation but that the most exciting parts of their numerical results correspond to biologically implausible conditions (as discussed above). However as far as the novelty of their approach is concerned the work of Dieckmann and Doebeli has indeed been very important. Although their claims about the ease with which sympatric speciation can happen have been proved too optimistic, the concrete results they have obtained represent an important contribution to modern speciation theory. Still, the unyielding insistence of the partisans of ''adaptive dynamics'' and ''adaptive speciation'' on the validity of the original claim about sympatric speciation occurring easily, although understandable on a personal level, is not productive or stimulating anymore. I note that other papers claiming that sympatric speciation driven by frequency-dependent selection occurs easily are plagued with similar problems (Gavrilets 2004). Therefore, in spite of significant advances in speciation research, as far as solid theoretical evidence is concerned, not much has really changed with regard to strengthening the case for sympatric speciation. However the claims made by some theoreticians have indeed became much stronger and bolder than previously made and these claims are often accepted by biologists at face value (Tregenza and Butlin 1999; Butlin and Tregenza 2005).

Doebeli et al. (2005) are right that the last few years have seen tremendous progress in theoretical speciation research (summarized in Gavrilets 2004). The work on ''adaptive speciation'' (Dieckmann et al. 2004) represents a significant part of this effort. There have been numerous, important advances in empirical studies as well (summarized in Coyne and Orr 2004). As a result of these efforts a solid quantitative theory of speciation is emerging now. This is indeed a very exciting time for speciation research.

So, what are the conditions for sympatric speciation as identified by theoretical research? These are: (1) strong combined effects of disruptive selection and nonrandom mating; (2) strong association of the genes controlling traits subject to selection and those underlying nonrandom mating; (3) high levels of genetic variation; and (4) the absence of costs of being choosy.

One of the easiest ways for sympatric speciation to occur is when there is a ''magic trait,'' a trait that is both subject to disruptive selection and simultaneously controls nonrandom mating. A second route to sympatric speciation is provided by habitat selection, when organisms evolve stronger and stronger preferences for specific habitats with mating taking place within preferred habitats (e.g., Bush 1969; Diehl and Bush 1989; Fry 2003; Johnson et al. 1996).

Mathematical models clearly show that under certain, biologically reasonable conditions sympatric speciation, in general, and ''adaptive speciation,'' in particular, are indeed possible. Why then are there so few cases where sympatric speciation is strongly implicated? For example, in their recent volume on speciation Coyne and Orr (2004) list only three such cases: tilapiine cichlids in the crater lakes of Cameroon (Schliewen et al. 1994), Arctic charr in Lake Galtabol in Iceland (Gíslason et al. 1999), and parasitic fig wasps in the genus Apocryptophagus (Weiblen and Bush 2002). There are two possible answers. First, sympatric speciation might be very difficult to distinguish from other alternatives. The other possibility is that conditions for sympatric speciation as identified by mathematical models are rarely satisfied in natural populations. In any case, the theory of sympatric speciation is arguably the most developed part of theoretical speciation research. Incorporating theoretical insights into empirical work will be a crucial step towards assessing the importance of this process in nature.

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