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What We Have Also Learned: Adaptive Speciation is Theoretically Plausible

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What we have also learned:

Adaptive speciation is theoretically plausible

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In a recent article in Evolution entitled “Models of speciation: what have we learned in 40 years?” Gavrilets (2003) aimed at reviewing the insights that evolutionary biologists have gleaned from mathematical models of speciation over the past decades. Despite this nominal ambition, there have been important developments in speciation research that were barely touched on in Gavrilets’ review.

Our aim here is not to point out factual errors in Gavrilets’ article, but to highlight crucial omissions. In particular, we focus on the innovations brought about by research into adaptive speciation, which in our opinion have received unduly short shrift in Gavrilets’ article. In general, the past years have seen a systematic shift in speciation research from the traditional emphasis on geographical patterns of speciation to a broader perspective of stressing the mechanisms and processes of evolutionary diversification (e.g., Schluter 2000, Kondrashov 2001, Mallet 2001, Via 2001). These processes include adaptive speciation, in which the splitting of lineages is an adaptive response to disruptive selection driven by biological interactions. Based on the modeling effort of a whole group of scientists it has by now become clear that adaptive speciation is a plausible evolutionary process in many different evolutionary scenarios (e.g., Metz et al. 1996, Doebeli 1996, Meszéna et al. 1997, Geritz et al. 1998, Kisdi 1999, Dieckmann and Doebeli 1999, Higashi et al. 1999, Kondrashov and Kondrashov 1999, Kisdi and Geritz 1999, Drossel and McKane 2000, Geritz and Kisdi 2000, Doebeli and Dieckmann 2000, Law et al. 2001, Kaneko and Yomo 2002, Mizera and Meszéna 2003, Doebeli and Dieckmann 2003, Van Doorn et al. 2004).

Adaptive speciation requires ecological contact between the diverging lineages and is therefore often equated with sympatric speciation, even though disruptive selection can also be a potent driver of speciation in parapatry. The possibility of adaptive speciation has been dismissed by Mayr (1963) and Dobzhansky (1970) as a plausible alternative to speciation through isolation by distance. The question of whether speciation under conditions of ecological contact, without isolation by distance, is a theoretically plausible evolutionary process hinges upon two key factors: first, on the ecological conditions under which frequency-dependent interactions are likely to generate disruptive selection, and second, on the evolution of assortative mating mechanisms in populations experiencing disruptive selection.

Investigating, by means of models, the ecological conditions under which sympatric speciation can occur has a long tradition that started with Maynard Smith (1966). The bulk of such models rely on rather simple genetic and ecological assumptions, typically involving two discrete ecological character states corresponding to two discrete ecological niches, and one or two loci determining mate choice (see Kawecki 2004 for a review). The model by Udovic (1980) that Gavrilets discusses in his article is an example of this class of models, as are most models for sympatric host-race formation (e.g., Diehl and Bush 1989, but see Fry 2003). It is known that the conditions for the maintenance of disruptive selection are restrictive in such models (Kawecki 2004). Together with the fact that the ecological assumptions in these models often appear to be rather special anyway, this has contributed to the perception that the origin and maintenance of diversity due to frequency-dependent selection requires special circumstances (e.g., Kassen 2002).

Extending earlier approaches toward more realistic (and, at the same time, more general) ecological settings by introducing the notion of competitive speciation, Rosenzweig (1978) provided a conceptual framework for thinking about how frequency-dependent selection on quantitative characters determining the utilization of continuously distributed resources (or niches) could lead to adaptive diversification. However, this promising line of research was rarely taken up in subsequent mathematical models of speciation, with Seger (1985) and Doebeli (1996) representing two of the few exceptions. A second line of research was opened by Christiansen (1991), Brown & Pavlovic (1992), and Abrams et al. (1993), who showed how the evolution of quantitative characters driven by frequency-dependent ecological interactions can converge on points in phenotype space at which selection turns disruptive. However, at the time these seemingly disparate examples were not yet recognized as special cases of a general principle. Moreover, these studies did not actually address the problem of speciation, restricting attention to the emergence of disruptive selection.

Even if a population does experience persistent disruptive selection, adaptive speciation in sexual populations requires the evolution of assortative mating mechanisms. Assortative mating can either be directly based on the ecological trait that is under disruptive selection, or it can be based on ecologically neutral marker traits, a distinction that corresponds to the 1-allele and 2-allele models of Felsenstein (1981) (for reviews see Kirkpatrick and Ravigné 2002, and Dieckmann and Doebeli 2004). When assortative mating is based on marker traits, a linkage disequilibrium between these marker traits and the ecological trait must develop for assortativeness to be able to latch onto the ecological trait. It has long been thought that this requirement significantly hinders adaptive speciation (Felsenstein 1981).

However, in recent years substantial progress has been made with regard to both understanding the ecological conditions of adaptive diversification, and the evolution of assortative mating mechanisms. In particular, we think that fundamental advances have been made with regard to the first aspect: the mathematical theory of adaptive dynamics (Metz et al. 1992, 1996, Dieckmann and Law 1996, Geritz et al. 1997, 1998) has provided a general framework for studying the emergence of disruptive selection induced by ecological interactions, which is embodied by the concept of evolutionary branching (Metz et al. 1996, Geritz et al. 1998). Evolutionary branching points are phenotypes characterized by a set of general and simple mathematical conditions that determine when directional selection can lead to disruptive selection and, further, to the emergence of protected dimorphisms. These conditions can be applied to any particular ecological scenario that may underlie the adaptive evolution of quantitative traits. Therefore, the concept of evolutionary branching serves as a potentially unifying principle for identifying the ecological conditions of adaptive diversification. Based on this principle, a multitude of theoretical studies in different evolutionary contexts have provided analytical results about the conditions under which adaptive splitting is likely to occur; see Kisdi and Gyllenberg (2004) for an overview of pertinent studies. Thus, adaptive dynamics theory allows us to discover the potential richness of adaptive speciation processes: based on the analytical conditions required for evolutionary branching it has become clear that ecological conditions for adaptive diversification are, as far as we can tell from theoretical studies, truly ubiquitous (see also Doebeli and Dieckmann 2000).

With regard to the second aspect of adaptive speciation, i.e., the evolution of assortative mating and reproductive isolation, two studies by Kondrashov and

Kondrashov (1999) and by Dieckmann and Doebeli (1999) have shown that in models with more realistic genetic assumptions than were used earlier on, adaptive speciation is a plausible process, even when only allowing for indirect assortative mating based on ecologically neutral marker traits. Thus, the conditions for the evolution of assortative mating under frequency-dependent disruptive selection are clearly less restrictive than earlier, simpler models had suggested. It also turns out that this conclusion is robust with regard to various changes in model assumptions, including costs of assortative mating (Bolnick 2004, Doebeli and Dieckmann 2004, Doebeli 2004).

The flurry of recent theoretical papers on the possibility of adaptive speciation reflects the fact that evolutionary biologists from all walks have started to realize that frequency-dependent selection can induce adaptive diversification, and that requirements for such processes are less restrictive than past dogma had us believe (e.g., Via 2001, Turelli et al. 2001). In his review, Gavrilets questions the value of the corresponding "dozens of new modeling papers" by suggesting that it is obvious that "selection promotes speciation". However, only a short while ago the possibility of adaptive speciation seemed far from obvious to many evolutionary biologists. Traditionally, only two mechanisms were considered through which selection could facilitate speciation: first, local adaptation in geographically segregated populations might accelerate the build-up of reproductive incompatibilities due to pre- or postzygotic isolation mechanisms, and second, reinforcement upon secondary contact might enhance an already existing level of reproductive isolation (see, e.g., the review by Turelli et al. 2001). Overcoming this unnecessarily narrow perspective on the interplay between adaptation and speciation required exactly the flurry of papers that Gavrilets bemoans, and the extent of this research activity is simply a consequence of speciation research being freed, after decades, from what one might portray as the ‘shackles of allopatry.’

In our opinion, the big news in recent speciation research is that many different ecological selection scenarios can easily give rise to selection pressures under which adaptive speciation is likely to occur. Understanding how these selective scenarios emerge from biological interactions is as important as understanding how the ensuing split into reproductively isolated subunits unfolds genetically. Ignoring this by focusing solely on traditional population genetic approaches and on traditional geographical classifications does not do justice to the exciting and dynamic state of the field. In particular, resurrecting an ecological perspective on speciation holds many promises for tying in speciation research with modern empirical and experimental approaches (e.g., Schluter 1994, Rainey and Travisano 1998, Schliewen et al. 2001, Friesen et al. 2004).

Contrary to what Gavrilets alleges in his review, the recent modeling efforts have indeed led to many analytical results. In fact, adaptive dynamics theory is exactly the kind of framework that yields analytical results similar to those presented by Gavrilets (2003) in his last example, and it is able to deliver such insights in a vast variety of different ecological and behavioral settings (see, e.g., Metz et al. 1996, Geritz at al. 1998, Kisdi and Geritz 1999, Doebeli and Dieckmann 2000). This is what one would want from a general theory. The bulk of analytical results obtained so far concern the ecological conditions for adaptive diversification, i.e., the existence or not of evolutionary branching points. Analytical results concerning the evolution of assortative mating mechanisms in multi-locus models for sexual populations are generally hard to come by. However, it should be pointed out that extensive numerical simulations can also yield complete classifications of system behavior (e.g., Doebeli and Dieckmann 2003), and can lead to statements that are just as universal as those derived by purely analytical means. Overall, given the many analytical results about conditions for diversification obtained using adaptive dynamics theory, we cannot agree with Gavrilets' assessment that "What is missing in the theoretical speciation research are general and transparent analytical results comparable to those in other areas of theoretical population genetics and ecology." Besides the fact that we now have a comprehensive mathematical framework that explains why adaptive diversification should be a ubiquitous and robust process, general analytical results have been obtained both for ecological and for sexual selection (e.g., Doebeli and Dieckmann 2000, Van Doorn et al. 2004).

Many empiricists have welcomed these new theoretical developments. Results from adaptive dynamics theory have shed new light on existing empirical work (e.g., Schluter 1994, Schliewen et al. 1994, Rosenzweig et al. 1994 (see Doebeli 2002), Johanneson et al. 1995, Skúlason et al. 1995, Treves et al. 1998, Rainey and Travisano 1998, Schliewen at al. 2001, Jiggins and Mallet 2001, Jones et al. 2003), and have inspired new empirical work that tests the theoretical predictions, both by analyzing existing data (e.g., Bolnick et al. 2003) and by using evolutionary experiments (e.g., Bolnick 2001, Friesen at al. 2004).

In addition, having available a general theoretical framework allows us to compare adaptive speciation with other processes of evolutionary diversification, such as the evolution of sexual dimorphism (Bolnick and Doebeli 2003, Van Dooren et al., submitted) or the evolution of ecological niche widths (Egas et al., submitted, Ackermann and Doebeli, submitted). With time, these efforts are likely to yield a fairly complete picture about the likelihood of adaptive speciation in various scenarios of ecological and sexual selection. In the end, theoretical advances have to be brought to fruition by modifying general theory so that it yields models that are applicable to particular situations. A multitude of models is needed to reflect the complexity of speciation, and specificity is not a problem if the models can be understood within a common conceptual framework. Excising such healthy pluralism from speciation research would seem unwise.

In this note, we did not endeavor to reflect all of theoretical speciation research. Instead we took a necessarily biased view by concentrating on the innovations brought about by research into adaptive speciation. It has become clear that the traditional geographical classification of speciation modes is no longer appropriate to capture the essential complexity of many speciation processes (e.g., Mizera and Meszéna 2003, Doebeli and Dieckmann 2003). By emphasizing adaptive *processes* rather than restricting attention to biogeographical *patterns* of diversification, theoretical and experimental speciation research have taken off again to new shores. These exciting developments were ignored in the review by Gavrilets. There are other omissions in Gavrilets' article, most notably perhaps the body of theory pertaining to the problem of reinforcement (e.g., Liou and Price 1994, Kirkpatrick and Servedio 1999, Servedio 2000). Reinforcement is of fundamental importance for many processes of ecological speciation as defined by Schluter (Schluter 2000; see also the Introduction in Dieckmann at al. 2004), and is related to the problem of the evolution of assortative mating mechanisms in processes of adaptive speciation. This further illustrates that Gavrilets' adherence to an old geographical classification of speciation that is fraught with problems, and the omission of whole bodies of work that have reinvigorated speciation research in the last decade, led to an unproductive bias on the representation of the field. While there is nothing wrong with Gavrilets reviewing his own contributions to speciation theory, which are substantial, we feel that a broader representation of an exciting and reinvigorated field would have been appropriate.

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