COMMENTARY

Adaptive dynamics: the continuity argument

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In reply to the Target Review by Waxman & Gavrilets (2004), I wish to explain why I consider adaptive dynamics as something simple, understandable, robust and beautiful. Adaptive dynamics, as I see it, is a continuity argument. The following statement will be referred to here as the 'Continuity Tenet':

Relative abundance of similar strategies has little effect on the adaptive landscape.

First, note that this statement makes sense only for a continuous strategy (phenotype, trait) space. This raises the single most important assumption of adaptive dynamics: we are talking about a continuous trait (for simplicity, I will consider a single one) and the small evolutionary changes of it. We can use a continuity argument only in the case of continuity, after all. (But see Meszéna & Szathmáry, 2001 about the delicate interplay between the continuous phenotype and the sequence space of the genotype).

Secondly, note the mathematical nontriviality of the simple-looking statement. If someone intends to formalize it, he/she should consider the interactions of the populations (i.e. of their combined population dynamics) of several strategies, which are 'similar', i.e. the difference between them – in all respects – goes to zero. Forget it for the purpose of this reply. I am talking to common sense here.

Thirdly, note that the 'Continuity Tenet' is self-evident. It is just inconceivable that it is false. Can anyone imagine a significant dependence of the fitness landscape on the relative abundance of phenotype A and phenotype B, when the only difference between them is that their optimal size of food differs by 1 μm? Probably A and B will not even be recognized as different.

Let us accept the 'Tenet' and talk about its consequences. We will assume large population sizes, which allow us to use a deterministic treatment. As ecology-dependent selection tends to be complicated, we will start by considering an asexual context.

Consequence 1

Invasion of a rare type against a resident implies that the invader will eventually win, and oust the resident, provided that the fitness gradient is nonzero and the two

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strategies are sufficiently similar. If the two strategies are *not* similar, initial invasion predicts nothing because the increasing abundance of the invader may change the situation such that its advantage is lost. However, if they are similar, the 'Tenet' guarantees that the direction of the fitness gradient will not be reversed by the increase of the invader. That is, the initial advantage survives until the final victory. This answers the questions raised in the 'What is the local fitness gradient?' section of the review from the common sense point of view. The reviewers are right, the formal proof is still missing from the literature, but it is coming (Geritz, in press; F.J.A. Jacobs, J.A.J. Metz, S.A.H. Geritz and G. Meszéna, in preparation).

Consequence 2

Consider now an arbitrary population, sexual or asexual, with a sufficiently small, but nonzero variance. Then, it will evolve in the direction of increasing fitness, with or without frequency dependence. While this statement looks trivial, it is not. It would not be true without the validity of the 'Continuity Tenet'. Specifically, see Dieckmann & Law (1996) for the gradient dynamics for mutation-limited asexual populations. It is analogous to, but different from, the Lande (1976) equation of population genetics.

Surprise 1

From the intuitive point of view, the most surprising feature of frequency-dependent selection is that directional evolution towards increasing fitness may end up in a local minimum, instead of the maximum, of the fitness. We need to de-learn our notion of a fixed fitness function to accept it. Ecology helps. Being *different* from the rest of the population may be so advantageous that the majority strategy is a fitness minimum, even in cases when it would be an optimum without the presence of the population. I consider the discovery of this possibility, which predates the emergence of adaptive dynamics, as the single most important contribution in understanding frequency dependence. As far as I understand, the discovery was made by several people independently. I am not sure whether the following list is complete: Eshel (1983), Taylor (1989), Christiansen (1991), and Abrams *et al.* (1993).

From a strictly formal point of view, the possibility of convergence to a fitness minimum is not a result, but a *lack* of it. If evolution can change the adaptive landscape on the way, there is no reason to conclude that we should reach a local maximum. While frequency dependence should be weak *locally*, it may be strong enough to affect the *global* outcome.

Consequence 3

The argument for Consequence 1 loses its validity when the fitness gradient becomes zero, i.e. at the 'singular'

points. An arbitrarily small change can tilt the horizontal fitness landscape in either direction. Initial increase no longer guarantees the final outcome. In particular, two arbitrarily similar strategies may be able to coexist near to the singular strategy, both of them invading the other, when rare. Nevertheless, we can reuse the argument for the *curvature* of the fitness function, which is supposedly nonzero. This leads to the classification of the singular points (Geritz *et al.*, 1997, 1998). Especially, strategies near to a fitness maximum evolve towards each other, while strategies near to a fitness minimum evolve away from each other. After Surprise 1, this is a highly nontrivial result of the general theory (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998). See Meszéna *et al.* (2001) for the comparison with matrix games, where the linearity of the fitness function, i.e. the zero curvature, introduces peculiarities.

Surprise 2: evolutionary branching

As a result of Consequence 3, an asexual population that has evolved to a fitness minimum will branch and the two branches will evolve away from each other. Then, adaptive dynamics argumentation can be applied, again, to the branches. This is the other big thing. The people who recognized Surprise 1, usually also expected something like this. However, it was the great achievement of my colleagues (Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998) to develop the theory of the (asexual) branching and note the generality and importance of the phenomenon. It is difficult to *not* see some resemblance to speciation, but I will come back to this point later.

Most importantly, this is the end of complications, as far as *continuous* evolution of *asexuals* is concerned. (And modulo continuity, differentiability, genericity, etc. assumptions, of course.) This is the beauty of adaptive dynamics. We do know that the properties of the singular strategies control the qualitative picture, and we do know the possibilities there. We cannot hope for a general analytic theory of frequency-dependent selection, just as we cannot hope for a general analytic solution for all possible dynamical systems. However, we have a fixed-point analysis for both of them, which helps a lot.

There are several ways to tell a single story. Often, it depends on personal taste. Meszéna *et al.* (1997) and Vukics *et al.* (2003) relied on this intuitive argument of continuity. To concentrate on the issue of singular point classification, and to avoid the mathematical complications, Geritz *et al.* (1997, 1998) *assumed* rare mutations (i.e. at most a single mutant is present at any specific time) and *assumed* that the outcome of the contest between two strategies is unequivocally determined by the mutual invasibilities. (That is, contrary to the reviewers' suggestion of the hidden assumptions, we were overcautious in these papers in stating the conditions.) The precise mathematical treatment of the continuity argument is coming (G. Meszéna, M. Gyllenberg, F.J.A. Jacobs and J.A.J. Metz, in preparation).

As the initial population size of the mutant population is small, we have to deal with 'Initial Stochasticity'. Fortunately, the situation is simple. As mentioned in the review, the mutant has a positive probability to invade if, and only if, the deterministic criterion of invasion is met. The actual probability is proportional to the invasion exponent. That is, stochasticity affects the speed of evolution, but not the location and the classification of the singular strategies. The issue was known to the adaptive dynamics community from the very beginning and mentioned already in Metz *et al.* (1996). It played a key role in Dieckmann & Law's (1996) development of gradient dynamics for mutation-limited asexual evolution. (Without taking into account the 'Initial Stochasticity', the speed of evolution would be independent of the slope of the landscape, which would be absurd!) Individual-based simulations (like those of Dieckmann & Doebeli, 1999; Mizera & Meszéna, 2003) took the effect into account automatically, so there was no reason to discuss stochasticity separately. I hereby acknowledge that we made a mistake in Meszéna *et al.* (1997). We simulated population growth deterministically without taking into account 'Initial Stochasticity'. This affects the exact shape of the branching curve on Figure 3, but nothing else. Figures in some other publications may suffer from the same problem. As the relative speed in different directions is an important issue for a multidimensional trait space, we discussed 'Initial Stochasticity' carefully in Vukics *et al.* (2003). The reviewers' claim, that the adaptive dynamics literature neglects the issue in an essential way, is overstated.

When we declare victory against frequency-dependent selection for continuous evolution of asexuals, the reader may feel that we have not yet met the real enemy. At the end of the day, we have to face the 'Complications of Sex', especially because of the appealing connection to speciation. Will sex change the conclusions? It is obvious/known that directional evolution, the end of evolution at a fitness maximum, and the possible arrival at a fitness minimum, are the same for asexuals and for sexuals (see, Taylor & Day, 1997 among others). However, the consequences of disruptive selection at a fitness minimum differ. They will depend crucially on genetic assumptions. In a random mating population frequency-dependent disruptive selection tends to increase and maintain genetic variance (Christiansen & Loeschcke, 1980). Some of us think that conditions may exist under which disruptive selection ends up in the development of reproductive isolation. Why not, when it selects against the intermediate types? Call the phenomenon, if it exists, 'Adaptive Speciation' irrespective of whether the process is sympatric or allopatric. The very first condition is to have an evolvable trait controlling the assortativity of mating, i.e. abandoning the assumption of random mating.

Does a 'branching' type singularity of adaptive dynamics predict adaptive speciation? Certainly *not*. First, because we have got a new problem: the evolution of sexual behaviour. It is not fully determined by the adaptive dynamics of the ecological trait, where our branching point has appeared. Secondly, because we lost the applicability of the 'Continuity Tenet' even for the ecological trait when we let the variance increase under disruptive selection. We can no longer suppose that only the first, or second, derivative of the fitness matter. (I thank Freddy Christiansen for pointing me to the second issue.) From a mathematical point of view, it is not mandatory for a 'practitioner of adaptive dynamics', as the reviewers call us, to believe in adaptive speciation. Note also that one can use all the arguments of adaptive dynamics in a continuous allele model (Kisdi & Geritz, 1999; Van Dooren, 1999). Then, it is a sexual application of adaptive dynamics, without caveats. Then evolutionary branching of the allelic value corresponds to an increase of variance of the population, instead of speciation.

I happen to be a fan of adaptive speciation. My reason is that ecology must be a part of the story, anyway. Without ecological segregation, the new species will not be able to coexist with the already existing one. (One can, of course escape from this requirement in a noncomplete model.) From a *biological* point of view, the simplest possible idea of speciation is the adaptive/competitive/ecological one (Rosenzweig, 1978): suppose that speciation is driven by adaptation to an empty niche. As one can learn from Christiansen (1988), ecology generates frequency dependence. In turn, frequency dependence may result in convergence to a fitness minimum, i.e. to disruptive selection. Things seem to fit.

For reasons that I do not fully understand, many people consider adaptive speciation as an extremely difficult possibility, at best. Turelli *et al.* (2001) state explicitly that the 'allopatric' theory of speciation goes well without mathematical modelling, because it is intuitively clear. However, ecological speciation supposedly depends on detailed mathematical analysis in a crucial way. But this tilts the playing field. While it is a widely accepted *assumption* of the allopatric theory that mutual infertility arises as a consequence of diverging evolution in allopatry, the reviewers asks whether the *emerging* reproductive isolation of Dieckmann & Doebeli (1999) is robust against introducing a cost of assortativity. The issue of adaptive speciation, i.e. equating asexual branching with sexual speciation, would be trivial by *assuming* that ecological divergence results in reproductive isolation automatically.

There are several models supporting the possibility of adaptive emergence of reproductive isolation. Matessi *et al.* (2001) is one of them – even if it was written to stress that the selective force should be strong enough. Obviously, the reviewers are right in claiming that any cost of assortativity will decrease the parameter range allowing speciation. I could suggest many other factors, which would either help or prevent adaptive emergence of reproductive isolation. But the same could be done for any evolutionary process. It will take several years to see the full picture, I am sure.

In particular, I do not think that the model of Dieckmann & Doebeli (1999) is the final word on the issue. Nevertheless, I am puzzled that the reviewers seem to suspect trivial-level mistakes in it. (I happen to know how clean and reliable the code behind this work is and how careful the authors are in avoiding the traps.) Why should it be a problem that they start the simulation with the maximal variance, when the maximal variance is the stable fixed point under disruptive selection (Bulmer, 1980, p. 171), anyway? Why should it be a problem that they chose a mutation rate higher than the natural one just to compensate for the fact that they use small population size and small number of loci for numerical convenience? When the whole model is far from the quantitative fidelity, anyway? Why should it be a problem that the model is not about generating variance, which is a solved problem, but about sorting it into different species, which is their topic? I am sure the authors of this model will falsify the 'easily falsifiable' hypothesis of the reviewers. But here the point is why are our intuitions so different?

Contrary to Turelli *et al.* (2001), I feel that ecological speciation is at least as intuitively appealing, simple and understandable, as anything else. (Nevertheless, it needs quantitative modelling, as anything else!) I am sure it is related to my involvement in adaptive dynamics. The behaviour of Occam's razor depends on whether one considers frequency-dependent selection and convergence to the fitness minimum something strange and complicated, or an elementary fact of ecology that is easy to interpret and which is under control. My version of Occam's razor implies studying the consequences of ecology-generated fitness landscape first. While adaptive dynamics does not imply adaptive speciation in any mathematical way, it is not an accident that some of the adaptive dynamicists support adaptive speciation.

As I consider adaptive dynamics something transparent, I disagree with the judgement of the reviewers about the 'hidden limitations and unconscious or implicit assumptions'. Of course, adaptive dynamics, as any other theory, has limitations in describing the real word. For instance, if speciation is a process driven by neutral evolution, then it has nothing to do with adaptive dynamics. Adaptive dynamics is, by definition, concerned with adaptive evolution. However, this is something different from the reviewers' claim that adaptive dynamics overlooks genetic drift, in its own context, as a hidden assumption.

Similarly, if the evolutionary process is dominated by a small number of large mutational steps, instead of a roughly continuous evolution of a trait, the simplification of the 'Continuity Tenet' does not apply. An exact

mathematical wording would require 'infinitesimal' mutational steps for the applicability of adaptive dynamics. The real-word-oriented translation is that 'it should be small in any relevant comparisons'. For instance, and most importantly, the mutation step size should be too small to jump to the other side of a fitness minimum, or the description cannot be based on gradient dynamics. Practitioners of adaptive dynamics meet this issue each day in each of their models. Again, this is not a hidden assumption, but the very essence of the approach.

Similarly, if the genetic details are important, then one should not attempt to describe the evolutionary process on the phenotypic level. In general, applicability of adaptive dynamics in a given context depends on the nature of the phenomenon we are investigating. If there is a disagreement on the biological essence of the speciation process, then we will disagree on the applicability of adaptive dynamics, of course. But this is natural; it has nothing to do with the supposedly hidden assumptions of adaptive dynamics.

As far as I understand, the theory itself is fairly stable now.

Last, but not least, I wish to apologize for the apparently arrogant nature of this commentary. Neither the expected length, nor the supposed style, allowed me an in-depth discussion of all the specific points the reviewers raised. I could not discuss technical details of the mathematical issues, either. My only goal was to express and motivate my general judgement: adaptive dynamics is transparent. I thank all of my colleagues for the rewarding years of learning together and the reviewers for the possibility of this exchange.

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