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Pluralism in Evolutionary Theory

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Contents

Pluralism in Evolutionary Theory

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The review by Waxman and Gavrilets (Waxman and Gavrilets 2005) illustrates the collision of different mindsets in evolutionary theory. These differences originate from the awe-inspiring complexity of the evolutionary process itself: evolutionary understanding critically depends on processes at many biological levels. Starting out with base pairs and their sequences, scholars of evolution have to consider – in the order of ascending biological complexity – alleles, quantitative allelic traits, physiological and morphological traits, life-history traits, demographic rates, fitness, changes in genotype frequencies, population dynamics, trait substitution sequences, and population bifurcations, to eventually arrive at the levels of ecological communities and the biosphere. It would appear that no other field of contemporary science sports comparable ambitions.

A plea for interfaced pluralism in evolutionary theory

As history abundantly illustrates, science successfully tackles challenges such as those encountered in the understanding of evolution by devising chains of theories that, step by step, traverse otherwise intractable ranges of complexity. Theories not appreciating the virtue of such level-based division of labor are bound to fail: nobody would seriously insist, for example, that phenomena in organic chemistry be explained in terms of quantum electrodynamics.

Yet, at times, one gets the impression that things are different in evolutionary theory: since quantitative evolutionary theory came into being by describing the dynamics of genotypes, there is a tendency to insist that all meaningful evolutionary models should be explicitly based at the level of genotypes and their dynamics. In practice this particular brand of 'level centrism' works best when attention is restricted to simplistic genotype-to-phenotype maps with simplistic phenotype-to-fitness maps. There certainly exist cases where genetic details are simple enough, and sufficiently well studied empirically, for genotype-to-phenotype maps to become thoroughly understood. Also phenotype-to-fitness maps may occasionally be straightforward: in animal and plant breeding, for example, complex ecological feedbacks on the evolutionary process may sometimes be tempered successfully through a breeder's tight control of the breeding environment. By contrast, in most natural settings – and certainly when it comes to long-term evolution – genetic detail is largely unknown and ecological complexity is mostly high. To insist, under such circumstances, on all evolutionary models being based on genotype dynamics would appear to be counterproductive.

Adaptive dynamics theory challenges such prescriptive stances by extending evolutionary game theory towards a dynamical theory of long-term evolution. This extension involves (a) accounting for all types of frequency- and density-dependent selection; (b) allowing for the stochastic and nonlinear dynamics of unstructured and structured populations; (c) considering continuous (not just mixed) strategies, metric characters, or quantitative traits; (d) describing dynamics driven by evolutionary innovations, as well as identifying and classifying the resulting evolutionary outcomes; and, perhaps most importantly, (e) deriving fitness from the underlying population dynamics. By contrast, more than 70 years after the Modern Synthesis, population genetics is still struggling to extend its gene-frequency-based models to incorporate the degrees of ecological complexity that are necessary for doing justice to long-term evolution and coevolution. (A cursory glance at how established textbooks of genetics treat frequency-dependent selection – increasingly recognized as being ubiquitous in nature – will help to appreciate the point.) In this constellation, adaptive dynamics theory may be perceived as playing down the relevance of population genetics. We think this perception would be unfortunate. Instead, it seems to be more productive to us to recognize that a diverse swath of complementary and mutually enhancing approaches is required for making progress with the diverse challenges posed by evolutionary theory.

To contribute to such progress, adaptive dynamics theory trades genetic for ecological detail. Since for questions of long-term evolution the former is almost always unknown, while the latter is essential, accepting this trade-off, and the associated focus at the phenotypic level of evolution, would appear to be a rational choice. New perspectives can thus be developed to complement previous theory and to foster a healthily diverse scientific discourse. It is because of its stance regarding this trade-off that adaptive dynamics theory at times jars with a more classical outlook, which had relegated these aspects to the fringes. At the same time, many evolutionary ecologists are thrilled by the innovative possibilities adaptive dynamics theory readily offers to them, thus underscoring the theory's innovative potential.

Having experienced the vigor that occasionally creeps into this debate, we suggest that evolutionary theory has a lot to gain from explicitly embracing a pluralism of approaches that are based, alternatively, on population genetics, quantitative genetics, adaptive dynamics, and evolutionary games. Along the astonishing spectrum from molecules to ecosystems, each of these approaches plays out its forte at different levels and for addressing different questions: population genetics is strongest in bringing out the evolutionary intricacies caused by specific genetic architectures, quantitative genetics excels at examining short-term responses to selection and breeding experiments, adaptive dynamics facilitates understanding the impacts of ecology on life-history evolution, and evolutionary games are most useful for exploring behavioral adaptations.

Pluralism, of course, must not inspire isolation. While separate traditions may be instrumental in nurturing diversity – occasionally defining temporary 'intellectual sandboxes' for innovative research – it is crucial that sufficient efforts be devoted to strengthening the interfaces. These are located, in general, where complexity steps up from one level to the next. A classical example is the science of the hydrogen molecule, which is poised right at the interface between (quantum) physics and (inorganic) chemistry. Clearly, connections must be forged from across both sides of such a disciplinary boundary if areas of fruitful overlap are to become as wide and as well understood as possible.

We now proceed to examine aspects of Waxman and Gavrilets' review (written by authors who have not contributed to the field they strive to portray) with this commendation of interfaced pluralism in mind. In fact, the tensions at the interface between complementary approaches to describing evolution are fully apparent in Waxman and Gavrilets' writing with regard to two fundamental aspects of evolutionary theory: the origin and maintenance of genetic diversity, and the definition of fitness and its dynamic consequences. Naturally, complementary approaches deal with these issues in different ways, and disciplinary biases can easily lead to misunderstandings and misinterpretations.

Origin and maintenance of genetic variation

Perhaps due their unfamiliarity with adaptive dynamics, Waxman and Gavrilets make a number of claims that require qualification. For example, their assertion that "Adaptive Dynamics methodology, based on using Eq. (1), predicts that polymorphism cannot be maintained when the singular point is locally stable" is fallacious. In fact, adaptive dynamics theory offers detailed methods for identifying and analyzing dimorphisms of this sort, at three different levels. (1) All ecologically stable dimorphisms are identified by reflecting a pairwise invasibility plot about its main diagonal and superimposing the resulting sign structure of invasion fitness onto the original one. All areas of dimorphic trait space in which the mutual invasion fitness of the two morphs is positive are thus readily identified geometrically. (2) To find out where gradual evolution in dimorphic trait space is expected to end up, i.e., to analyze dimorphic convergence stability, evolutionary isoclines (curves along which the local fitness gradient of one trait vanishes) are added to these plots (e.g., Geritz et al. 1998, 1999). (3) Finally, evolutionary stability at a dimorphic evolutionary attractor is ascertained by considering the sign of invasion fitness in its vicinity. Corresponding analytical techniques for higher-dimensional analysis are readily available (Meszéna et al. 2000; Leimar 2001). Also the fact that a "population does not necessarily approach a convergence stable equilibrium but can 'get stuck' at a polymorphic equilibrium away from the singular point" is, of course, recognized in adaptive dynamics theory (e.g., Geritz et al. 1999).

With regard to the origin of new genetic variation through mutation, the characterization of adaptive dynamics as being "based on the assumption that mutations occur rarely, and cause very small changes in existing phenotypic values" is not accurate. If the latter part of this claim were true, why would adaptive dynamics theory include pairwise invasibility plots as an important tool of analysis? Indeed, invasion fitness and pairwise invasibility plots are devised to assess the effects of mutational steps of arbitrary size. Also the assertion that "The phenotype of a mutation can take on any possible value and thus can range from $\infty > x > -\infty$" is clearly false for all phenotypic traits that are, by definition, restricted to finite intervals (e.g., Doebeli and Ruxton 1997; Parvinen et al. 2003). Furthermore, Waxman and Gavrilets claim that "In the Adaptive Dynamics literature to date, it has been implicitly assumed that beneficial mutations, i.e., those with a positive selection coefficient, will always initially increase in frequency, irrespective of the size of the selection coefficient, and irrespective of the copy number at which they occur." This is dramatically wrong. In actual fact, the dynamical description of trait substitution sequences in adaptive dynamics (e.g., Dieckmann et al. 1995; Dieckmann and Law 1996; Metz et al. 1996) is crucially based on recognizing and quantifying the fact that the typical fate of an advantageous mutant is to go extinct (Kimura 1983). This fact is also consistently emphasized in many other adaptive dynamics studies, e.g., Geritz et al. (1998, 1999). Similarly, the claim that "it is either implicitly or explicitly assumed that the distribution of the deviation of the mutant from the parental phenotype is independent of the parental phenotype" is erroneous, as a look at Dieckmann and Law (1996) will illustrate. Waxman and Gavrilets also overlooked that their observation that "once genetic drift is taken into account, the most significant mutations, as far as adaptation is concerned, may be those with intermediately sized effects" is accounted for in the description of evolutionary random walks by adaptive dynamics theory – with this very insight, in fact, serving as the basis of Equation (3.6) in Dieckmann and Law (1996).

Definition of fitness and resulting evolutionary dynamics

The notion of invasion fitness lies at the core of adaptive dynamics theory. Contrary to Waxman and Gavrilets' writing, invasion fitness s is defined as the long-term per capita growth rate of a rare variant in the environment determined by one or more residents (Metz et al. 1992). For any resident phenotype x this implies $s(x, x) = 0$, rather than $s(x, x) = 1$. While the discrete-time convention adopted by the authors is of course also valid (if more cumbersome), their unfaithful characterization of the existing literature might confuse some readers. Also the statement "The function $s(y, x)$ governs the dynamics of the frequency of the mutants" is incorrect, since what s *is* governing directly is the dynamics of mutant density (or abundance), not its frequency. Similar sloppiness is apparent when, at various places in their review, Waxman and Gavrilets use the inaccurate term "locally stable" when they mean 'locally evolutionarily stable'. This fosters confusion when, as in adaptive dynamics theory, several stability notions have to be considered in parallel.

In this context, the authors' admonition that practitioners of adaptive dynamics "should be more careful in inventing new terms for old concepts" sounds a bit overblown. The only underpinning for this claim comes from the authors' advice to refer to an evolutionarily singular strategy, one of the key concepts of adaptive dynamics theory, as a "stationary point", an "equilibrium point", or a "saddle point". The mere fact that Waxman and Gavrilets cannot decide themselves which of these three alternatives they actually mean to recommend already makes it obvious that the alternatives are not without problems either. In fact, this terminological misgiving touches on a key feature of adaptive dynamics. The criteria for evolutionary branching (Geritz et al. 1997) and the canonical equation of adaptive dynamics (Dieckmann and Law 1996) together result in the coupling of dynamical systems of different dimensions: a trait combination that happens to be a stable (or stationary) equilibrium point of n-dimensional adaptive dynamics is a saddle point of the corresponding $(n+1)$-dimensional adaptive dynamics, if and only if that combination is an evolutionary branching point. Using the notions 'stationary point' or 'equilibrium point' would also be inaccurate for another reason: evolutionarily singular strategies can be identified based on the geometry of pairwise invasibility plots alone, without considering any dynamical system. It is important to appreciate these subtleties before recommending a particular terminology.

One reason why Waxman and Gavrilets can give a relatively simple account of adaptive dynamics theory is that their review glosses over some of the more complex issues arising in realistic models. In particular, evolution often involves multiple traits: in such situations, the appealing geometric tools of one-dimensional adaptive dynamics must be complemented by suitable analytical consideration. This has led to two important lines of theory. First, the evolutionary outcomes in higher-dimensional trait spaces need to be classified according to a scheme that goes beyond what the review describes in its Table 1 (Meszéna et al. 2000; Leimar 2001). Second, the transients and outcomes of multi-dimensional adaptive dynamics are described by the canonical equation of adaptive dynamics (Dieckmann and Law 1996), which is derived as a deterministic approximation of the stochastic process resulting from trait substitution sequences (see also Leimar 2001; Champagnat et al. 2001; Durinx and Metz 2005). Only through this derivation can we understand (i) why, in mutation-limited adaptive dynamics, the rate of evolutionary change happens to be proportional to the local fitness gradient and the resident population size, and (ii) under which conditions the rate of mutation-limited evolution is independent of the partitioning of growth rates into birth and death rates – two insights that are far from obvious.

The entire review also glosses over the notion of ecological equilibria, or of more general ecological attractors, which lies at the very heart of an understanding of invasion fitness (e.g., Metz et al. 1992; Rand et al. 1993; Dieckmann and Law 1996; Jacobs and Metz 2003; Gyllenberg et al. 2003). The consequences of this omission become particularly evident in statements like "The movement downhill does not imply that the population experiences any fitness loss but rather reflects the resetting of fitnesses so that new resident population has a fitness of unity". The authors' cryptical allusion to the "resetting of fitnesses" is rooted in the traditional perspective of fitness as being defined independently of a population's resident traits and its currently attained ecological equilibrium. In actual fact, this "resetting" is nothing else than the inevitable and perfectly natural consequence of frequency- and/or density-dependent ecological interactions.

Waxman and Gavrilets suggest that when "fitness functions are not continuous functions of mutant frequency, the frequency of mutant phenotypes cannot be neglected – even initially – and may have a significant influence on the dynamics of the population. We know, however, of no concrete examples of this and it might be interesting to see this pursued further." This consideration is not well informed, for two reasons. First, the continuity of fitness functions is irrelevant here (since invasion fitness is always defined in the limit of mutant density approaching zero). Second, it should be noted that spatial ecological settings with limited dispersal provide natural examples of the type the authors refer to as being outside their knowledge: in such settings mutant individuals tend to interact strongly even while they are globally still rare. In fact, any form of group selection relies on this very principle, as a suite of studies based on adaptive dynamics theory have illustrated (e.g., van Baalen and Rand 1998; Metz and Gyllenberg 2001; Le Galliard et al. 2003).

The evolutionary dynamics resulting for a particular invasion fitness are primarily governed by the fitness gradient, $\frac{\partial}{\partial y} s(y,x)|_{y=x}$. In this context, the statements "gradient type dynamics has been well established in population genetics […] yet it is treated as a new development in Adaptive Dynamics" and "Such gradient-type dynamics are analogous to those studied in standard population genetics", referring to the canonical equation of adaptive dynamics (Dieckmann and Law 1996), are about as meaningful as saying that the plus signs used by economists are analogous to those used by physicists. Gradient dynamics are merely a generic type of dynamical system, whereas the biological mechanisms underlying such dynamics in population genetics and adaptive dynamics fundamentally differ. Similarly, a statement like "quantities such as fitness – a primarily population genetics concept" reflects an attitude that is perhaps akin to that of Richard Lewontin (1982), who, more than 20 years ago, decided to bestow his approval on evolutionary game theory because it "lies totally within the standard genetic structure of population genetics". Since fitness is realized by ecology in action, the need for an ecologically informed approach towards its definition seems incontrovertible.

Conclusions

In our view, many of the inaccuracies and omissions in Waxman and Gavrilets' review can be attributed to not acknowledging the necessity for pluralism in evolutionary theory. With less favoritism towards population genetics theory, and a more open mind to theoretical innovation, it would have been possible to provide a more accurate review of adaptive dynamics. For example, if Waxman and Gavrilets write that "It would be especially interesting to see a comprehensive comparison of empirical data and the corresponding predictions of Adaptive Dynamics", they are of course correct, since such a statement holds for all good science. Yet, such proclamations should be made with care so as not to denigrate the development of integrative and flexible theoretical frameworks, an ambition reflected also in Waxman's and Gavrilets' own publication records. In a similar vein, complaints about allegedly "hidden limitations and unconscious or implicit assumptions" and about the authors' impression that "quite a lot of the work in the literature on Adaptive Dynamics relies on numerical simulation" are questionable, especially since adaptive dynamics theory is the source of analytical tools, underpinned by explicit assumptions, that enabled a degree of generality that precursor theories could not achieve. Also, the sweeping allegation that "practitioners should be more open to referencing relevant recent work on evolutionary dynamics" cannot but be interpreted as patronizing. Waxman and Gavrilets refer to only one instance to back up their indiscriminate censure: the fact that previous work on parapatric speciation (Endler 1977; Caisse and Antonovics 1978; Moore 1981) "apparently was missed" by Doebeli and Dieckmann (2003). This is not very convincing since the article in question is a *Nature* paper with well-known restrictions on citation numbers and since Endler's work *was* actually quoted in that article.

Despite our reservations, and following the spirit of the discussions at the beginning of this commentary, we believe that Waxman and Gavrilets ought to be congratulated for their courage of serving as intermediaries, helping to bolster communication between the fields of population genetics and adaptive dynamics. There clearly is a need for strengthening the interface between these disciplines. It is certainly not a coincidence that Waxman and Gavrilets' article devotes much attention to speciation processes. We think that, in fact, speciation could assume a prominent role as the 'hydrogen molecule of evolutionary theory': genetic and ecological considerations are so inexorably intertwined at this interface that the necessary bridge-building is a genuinely rewarding challenge from both ends. It is therefore deplorable that Waxman and Gavrilets forewent backing up any of the criticisms voiced in the belligerent Section 5 of their review with results. An accompanying commentary (Doebeli and Dieckmann, this issue) refutes these unsubstantiated allegations.

If one is optimistic, one might take the article by Waxman and Gavrilets as a signal that population genetics is gradually opening itself to the promises of ecologically informed evolutionary theory. A quarter of a century ago, evolutionary game theory, notwithstanding its admirable achievements, did not quite succeed in perturbing traditional population genetics enough in the direction of ecological realism. Our hope is that, perhaps, adaptive dynamics theory will be luckier.

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