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Pluralism in Evolutionary Theory

Dieckmann, U. and Doebeli, M.

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Interim Report

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Pluralism in Evolutionary Theory

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The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

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Contents

Abstract.....	1
A plea for interfaced pluralism in evolutionary theory	1
Origin and maintenance of genetic variation.....	3
Definition of fitness and resulting evolutionary dynamics.....	4
Conclusions	5
References	7

Pluralism in Evolutionary Theory

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The review by Waxman and Gavrillets (Waxman and Gavrillets 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

47 underlying population dynamics. By contrast, more than 70 years after the Modern Synthesis,
48 population genetics is still struggling to extend its gene-frequency-based models to incorpo-
49 rate the degrees of ecological complexity that are necessary for doing justice to long-term
50 evolution and coevolution. (A cursory glance at how established textbooks of genetics treat
51 frequency-dependent selection – increasingly recognized as being ubiquitous in nature – will
52 help to appreciate the point.) In this constellation, adaptive dynamics theory may be perceived
53 as playing down the relevance of population genetics. We think this perception would be un-
54 fortunate. Instead, it seems to be more productive to us to recognize that a diverse swath of
55 complementary and mutually enhancing approaches is required for making progress with the
56 diverse challenges posed by evolutionary theory.

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

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

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

84 We now proceed to examine aspects of Waxman and Gavrillets’ review (written by au-
85 thors who have not contributed to the field they strive to portray) with this commendation of
86 interfaced pluralism in mind. In fact, the tensions at the interface between complementary ap-
87 proaches to describing evolution are fully apparent in Waxman and Gavrillets’ writing with
88 regard to two fundamental aspects of evolutionary theory: the origin and maintenance of ge-
89 netic diversity, and the definition of fitness and its dynamic consequences. Naturally,
90 complementary approaches deal with these issues in different ways, and disciplinary biases
91 can easily lead to misunderstandings and misinterpretations.

92 *Origin and maintenance of genetic variation*

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

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

136 *Definition of fitness and resulting evolutionary dynamics*

137 The notion of invasion fitness lies at the core of adaptive dynamics theory. Contrary to Wax-
138 man and Gavrilets' writing, invasion fitness s is defined as the long-term per capita growth
139 rate of a rare variant in the environment determined by one or more residents (Metz et al.
140 1992). For any resident phenotype x this implies $s(x, x) = 0$, rather than $s(x, x) = 1$. While the
141 discrete-time convention adopted by the authors is of course also valid (if more cumbersome),
142 their unfaithful characterization of the existing literature might confuse some readers. Also the
143 statement "The function $s(y, x)$ governs the dynamics of the frequency of the mutants" is in-
144 correct, since what s is governing directly is the dynamics of mutant density (or abundance),
145 not its frequency. Similar sloppiness is apparent when, at various places in their review,
146 Waxman and Gavrilets use the inaccurate term "locally stable" when they mean 'locally evo-
147 lutionarily stable'. This fosters confusion when, as in adaptive dynamics theory, several
148 stability notions have to be considered in parallel.

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

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

180 lution is independent of the partitioning of growth rates into birth and death rates – two in-
181 sights that are far from obvious.

182 The entire review also glosses over the notion of ecological equilibria, or of more general
183 ecological attractors, which lies at the very heart of an understanding of invasion fitness (e.g.,
184 Metz et al. 1992; Rand et al. 1993; Dieckmann and Law 1996; Jacobs and Metz 2003;
185 Gyllenberg et al. 2003). The consequences of this omission become particularly evident in
186 statements like “The movement downhill does not imply that the population experiences any
187 fitness loss but rather reflects the resetting of fitnesses so that new resident population has a
188 fitness of unity”. The authors’ cryptical allusion to the “resetting of fitnesses” is rooted in the
189 traditional perspective of fitness as being defined independently of a population’s resident
190 traits and its currently attained ecological equilibrium. In actual fact, this “resetting” is noth-
191 ing else than the inevitable and perfectly natural consequence of frequency- and/or density-
192 dependent ecological interactions.

193 Waxman and Gavrillets suggest that when “fitness functions are not continuous functions
194 of mutant frequency, the frequency of mutant phenotypes cannot be neglected – even initially
195 – and may have a significant influence on the dynamics of the population. We know, how-
196 ever, of no concrete examples of this and it might be interesting to see this pursued further.”
197 This consideration is not well informed, for two reasons. First, the continuity of fitness func-
198 tions is irrelevant here (since invasion fitness is always defined in the limit of mutant density
199 approaching zero). Second, it should be noted that spatial ecological settings with limited dis-
200 persal provide natural examples of the type the authors refer to as being outside their
201 knowledge: in such settings mutant individuals tend to interact strongly even while they are
202 globally still rare. In fact, any form of group selection relies on this very principle, as a suite
203 of studies based on adaptive dynamics theory have illustrated (e.g., van Baalen and Rand
204 1998; Metz and Gyllenberg 2001; Le Galliard et al. 2003).

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

220 *Conclusions*

221 In our view, many of the inaccuracies and omissions in Waxman and Gavrillets’ review can be
222 attributed to not acknowledging the necessity for pluralism in evolutionary theory. With less
223 favoritism towards population genetics theory, and a more open mind to theoretical innova-

224 tion, it would have been possible to provide a more accurate review of adaptive dynamics. For
225 example, if Waxman and Gavrilets write that “It would be especially interesting to see a com-
226 prehensive comparison of empirical data and the corresponding predictions of Adaptive
227 Dynamics”, they are of course correct, since such a statement holds for all good science. Yet,
228 such proclamations should be made with care so as not to denigrate the development of inte-
229egrative and flexible theoretical frameworks, an ambition reflected also in Waxman’s and
230 Gavrilets’ own publication records. In a similar vein, complaints about allegedly “hidden
231 limitations and unconscious or implicit assumptions” and about the authors’ impression that
232 “quite a lot of the work in the literature on Adaptive Dynamics relies on numerical simula-
233 tion” are questionable, especially since adaptive dynamics theory is the source of analytical
234 tools, underpinned by explicit assumptions, that enabled a degree of generality that precursor
235 theories could not achieve. Also, the sweeping allegation that “practitioners should be more
236 open to referencing relevant recent work on evolutionary dynamics” cannot but be interpreted
237 as patronizing. Waxman and Gavrilets refer to only one instance to back up their indiscrimi-
238 nate censure: the fact that previous work on parapatric speciation (Endler 1977; Caisse and
239 Antonovics 1978; Moore 1981) “apparently was missed” by Doebeli and Dieckmann (2003).
240 This is not very convincing since the article in question is a *Nature* paper with well-known
241 restrictions on citation numbers and since Endler’s work *was* actually quoted in that article.

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

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

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