COMMENTARY

Eight personal rules for doing science

J. A. J. METZ

Section Theoretical Biology, Institute of Biology, Leiden University, Leiden, The Netherlands and Adaptive Dynamics Network, Institute for Applied Systems Analysis, Laxenburg, Austria

1. On structures and predictions

Adaptive dynamics (AD) is not a scientific theory, but a mathematical framework for dealing with eco-evolutionary problems, based on a varied set of simplifying assumptions as a means of approaching problems of otherwise greater complexity. As such it may be compared with e.g. the theory of stochastic processes, or of differential equations. AD can make predictions only in a similar way to these theories: it lays bare consistent patterns in mathematical structures, some of which hopefully connect to the real world. Predictions largely come from specific models. AD studies the tools for analysing such models. Like in the theory of differential equations or bifurcation theory, a number of these tools already existed before the abstract theory took off. AD creates order on an abstract level, which in turn helps in constructing new tools. As far as the use of the newer tools is concerned, AD can be said to have contributed to predictions. Another class of predictions from AD arise from arguments on the frequency with which one may expect different situations to occur. A number of such predictions are present in my first paper on the subject (Metz *et al.*, 1996). These are repeated, with one correction and with a few others added, in Box 4.8 in Geritz *et al.* (2004). Two more general predictions are discussed in Metz & McCune (2004). These predictions mainly concern macro-evolutionary patterns, an area left singularly bare of predictions by the modern synthesis. It was precisely the longing for such predictions that started my personal search for the simplest possible dynamic extension of ESS theory, and thus got me hooked on AD.

2. On grouping people

There does not exist a well-defined AD community. There are presently at least three broad 'schools': around Tom Vincent and Joel Brown, based on differential equations, control, and game theory; around Peter Abrams, based on Lande's equation and differential

Correspondence: J. A. J. Metz, Section Theoretical Biology, Institute of Biology, Leiden University, PO Box 9516, NL-2300 RA Leiden, The Netherlands.
Tel.: +31 71 5274937; fax: +31 71 5274900;
e-mail: metz@rulsfb.leidenuniv.nl

equation based community models; and the Europeans, focussing on limit arguments for individual-based ecological stochastic processes, and on abstract dynamical systems arguments. But even these slightly more homogeneous groups cannot be considered well-defined communities. I pride myself, being one of its godfathers, on the diversity within the European group. In my opinion science should be as anarchic as possible, lest social ties or propriety get in the way of the uninhibited search for truth. Moralizing about group behaviour is improper and does not reflect the reality of the social situation.

Given my predilection for anarchy, below I only speak for myself, as others in the 'community' should speak for topics that are closer to their heart than they are to mine.

3. On the reaches of biological theory

I entered evolutionary biology sideways at a rather late stage in my career. My two original backgrounds are old-fashioned naturalism and relatively abstract mathematics. For a proof that these scientific disciplines combine seamlessly see e.g. Diekmann *et al.* (2003), Gyllenberg *et al.* (2003) and Durinx & Metz (2005). My own contributions to AD directly reflect these backgrounds. I care for the biological detail seen in the field and despair about the amount to which this detail is assumed away in most of the theoretical biological literature. I sincerely feel that biological complexity may be abstracted away, in the sense that it is proven that it matters little once a certain level of abstraction is reached, but should never be assumed away, e.g. by assuming that all individuals are equivalent, dying and giving birth at random, as is done in most differential equation models. This does not mean that the latter models are worthless as they may be valuable representatives of an equivalence class of models all showing the same phenomenon. As such, these oversimplified models are good tools for discovering phenomena. But their eventual justification should come from their embedding in a larger class of models, some members of which connect more directly to the real biological world.

When during my first summer holidays after graduation I read Crow & Kimura's (1970) book on population genetics, I was at the same time carried away by its mathematical beauty and abhorred by the extent to which real biology, as I saw it from my tent, was missing. It is this feeling of imbalance that has guided my choices over the years, up to my present involvement with AD. And, rather than trying to extend AD in the direction of population genetics, I prefer to work on its underpinning from the evo-devo side (e.g. Galis *et al.*, 2001, 2002; Galis & Metz, 2001, 2003), as I believe that, as far as long term adaptive change is concerned, such an extension may well be more conducive to producing relevant predictions than me as a newcomer adding to the already awesomely large body of population genetical literature.

4. On simplifications

The simplifying assumptions of AD are presently largely made at the genetic end, just as population genetics tends to make its simplifications at the ecological end. These assumptions are extensively discussed in the two papers (Dieckmann & Law, 1996; Metz *et al.*, 1996) that laid out the 'European research program'. One assumption is clonal reproduction. This assumption was made in order to concentrate on and treat in some generality the ecological side of evolutionary change, a side that I still feel to be underrepresented not so much in the specific as in the general theoretical evolutionary literature. The idea was that first identifying the evolutionarily relevant common properties of large classes of ecological processes would provide a good basis for slowly reintroducing more genetical detail. A purely ecological assumption made initially was the uniqueness of ecological attractors. Clearly, both assumptions, clonal reproduction and uniqueness of ecological attractors, can be considerably relaxed. However, it is easier to do so from an established reference platform. Presently, I and many other Europeans are working hard at determining the extent to which such a relaxation of assumptions can be effected (e.g. Geritz *et al.*, 2002; Jacobs & Metz, 2003; Geritz, 2004; Metz, in press). The second set of 'assumptions' referred to specifically in W&G are actually not assumptions as such but limit arguments. The difference is small, but relevant in the present context. An assumption delimits a class of models. A limit argument constructs a particular class of models from a larger or different class as a means of obtaining insight into this larger class. Judging the performance of limit models is done in two steps, with step 1 discussing the region of parameter space where the approximation does a good job, and step 2 discussing where in parameter space one expects particular real systems to be located. The two main limits used in AD are based on mutation limitation and phenotypic smallness of mutational steps. Interestingly, by embedding the AD models in a still larger class, step 2 for these limits also can be brought partially within the theoretical as opposed to the empirical realm. The picture emerging from constructional morphology and evo-devo is one of very high dimensional trait spaces and very ridgy fitness landscapes. Because of the high dimension of the trait space, the top of the ridges may be higher dimensional, although relatively low dimensional compared with the off-ridge directions. The slopes at the top of the ridges are the domain of ecology and thus of AD, whereas their overall location is largely ecology independent. The combination of this picture with an argument in the spirit of Fisher's argument on curvature effects in high dimensional spaces (Fisher, 1930; revived and extended by Rice, 1990), suggests that the parameter regions where the limit procedures favoured by AD work well, should contain their fair share of real cases, as by far the most mutations, and in particular those with large effect, end up in the fitness abyss.

5. On earth friendliness

I believe that scientific writing should be as compact as possible, within the constraints that adherence to mathematical truth and precision takes precedence. The goal is producing results and not cutting down trees. I am proud that there is little overlap between the content of my diverse publications. After I have written something, I prefer not to repeat it, but to rely on citations. This may be one reason why W&G believe that assumptions are left implicit; in the suites of papers of which I am co-author these assumptions are discussed carefully on the first occasion and after that are repeated only as compactly as possible. In a similar vein, I see citing primarily as a means for shortening papers; in particular, citing should not lead to extensions of the text just in order to connect it with remoter material. Here my background in mathematics shines through. What matters is that a paper contains a well-crafted consistent argument, relatively complete within its confines. Elucidating historical connections is best left to historians, who in general will do a better, or at least less biased, job.

6. On citing

Here are two concrete examples: (i) W&G feel that the AD crowd should cite what they consider precursors of ADs 'gradient dynamics'. Wright's gradient dynamics (Wright, 1937a,b) is defined on a space of gene frequencies as opposed to phenotypes. Russ Lande's gradient dynamics (Lande, 1976, 1982) deals with biologically similar problems but rests on a mathematically different foundation, as it considers a different limiting regime. If the connection is in the concept of gradient dynamics only, then priority goes to the physical and mathematical literature. However, the 'gradient dynamics' of AD is not a gradient dynamics at all, as the gradient is taken with respect to one of the variables in a function of two variables, whereas the dynamics takes place in the other of the two variables. So citing the older literature without further explanation is mathematically improper. When an explanation does not contribute to the intrinsic clarity of the arguments of a paper, then this explanation does not belong there, valuable although it would be were it published in a historical or review paper. (ii) I learned the use of Pairwise Invasibility Plots from van Tienderen & de Jong (1986), but they are present already in Matsuda (1985). Matsuda's PIPs I missed, for which I already apologized to him in person (I confess to preferring to roam novel territory in the few weeks that I have per year for research, instead of combing the older literature for potential predecessors, especially since in this literature the topics that have my main interest usually appear

as side issues only). Christiansen & Loeschcke's (1980) PIP I also initially was unaware of, but I was informed by Freddy. However, they present their PIP primarily as a parameter plot in a short-term evolutionary context, without overtly connecting it to the adaptive random walk. For me PIPs and the adaptive walk come as a package deal; my citing does not refer to the plot but to its use.

I admire the work of Ronald Fisher, J.B.S. Haldane, Sewall Wright, Ilan Eshel, Russ Lande, Peter Taylor and Freddy Bugge Christiansen, to name but a few of the great population geneticists. They did and do a marvellous job, and I very much enjoyed my efforts, to name one example, to make my way through Freddy's 1999 book (Christiansen, 1999). However, admiration is not a proper basis for writing scientific prose.

7. On ecological generality and mathematical elegance

The trick that AD uses to reach ecological generality starts with the introduction of the environment E as an intervening variable (actually, this 'variable' should be interpreted as a probability measure on time functions). This concept of environment is much more general than just a weighted average of population densities. Because of this trick invasion fitness can always be defined, also for stably fluctuating physiologically and spatially structured polymorphic resident populations, by substituting for E the ecological attractor for the resident types. The cost paid is that fitnesses are not defined for the overlapping transient polymorphisms that without mutation limitation occur during evolutionary transients, for these do not support well-defined stationary environments (under the very restrictive simplifying assumption of viability selection and nonoverlapping generations it is also possible to talk about fitnesses during population genetical transients, but these are instantaneous as opposed to overall fitnesses, and certainly not invasion fitnesses). The invasion fitness function s follows by eliminating the intervening variable E (AD workers most often use the symbol s for continuous time invasion fitness, for its allusion to a selection coefficient, whereas discrete time fitness is denoted as w; so $s = \ln(w)$. Below I will adhere to this tradition). Somewhat surprisingly this very general framework leads to a few very strong results because of the necessary presence of ecological consistency conditions like $s(x; x) = 0$ [$\Leftrightarrow$ $w(x; x) = 1$], $s(x_1; x_1, x_2) = s(x_2; x_1, x_2) = 0$, $s(y; x_1, x_2) = s(y; x_2, x_1)$, and in an evolutionarily singular point $s(y; x^*, x^*) = s(y; x^*)$. I appreciate W&G's start from the familiar world of population genetics textbooks. However, in so doing they play down utterly the beauty and ecological generality that comes from using no more than the simplest, undisputed ecological laws. They even go so far as to write about the fitness difference $w(y; x) - w(x; x)$, instead of $w(y; x) - 1$, or, better still, the sign-equivalent $s(y; x)$, ignoring that from the outset not only the concepts but also the notation of European AD were crafted to achieve the maximal economy of arguments and formulas (my preference for any particular notational system is necessarily context dependent. On other occasions the classical population genetical notation does a better job. However, one should never spurn the advantages a particular system may have for the job at hand).

8. On terminological precision

One of my goals in life is to make biology as exact a science as possible, on a par with physics and chemistry. I am (despite my great admiration for John Maynard Smith) still fighting a losing battle against the misnomer evolutionarily stable strategy. I was just lucky that the term Evolutionarily Singular Strategy, which was chosen for purely mathematical reasons, actually may serve as a minor weapon in this war. Although too much purism is objectionable, I should point out that evolutionarily singular points are not equilibrium points as is suggested by W&G. A point in case is a branching point. If the adaptive walk starts exactly in a branching point it will not stay there. The definition of an equilibrium point is: once there, and no extraneous noise, then stay there. W&G revert to apparent purism when it comes to the term branching point. Let me defend myself by pointing out that branching points are those points where ecologically branching can occur, which is not to say that it will occur. Whether it indeed occurs depends on nonecological factors like the genetic architecture. I have no watertight rules for naming concepts. One thing is clear although, when parsing names one has to account for the context (in the case at hand the focus on ecology). Otherwise, one may e.g. naively conclude that a random variable is normally distributed as it represents a measurement on a normal phenomenon.

Lest this comment ends on too negative a note, let me finish by saying that I am thankful to Sergey Gavrilets and David Waxman for the effort they took to read through and summarize the AD literature from their perspective. As we all unfortunately know too well, building bridges is not the easiest of jobs. And I for one am most thankful that they tried their hands on a job which I, focused as I am on arguments instead of people, never would have dared to tackle.

Acknowledgment

References

Christiansen, F.B. 1999. *Population Genetics of Multiple Loci*. Wiley, Chichester.

Christiansen, F.B. & Loeschcke, V. 1980. Evolution and intraspecific exploitative competition: I. One-locus theory for small additive gene effects. *Theor. Pop. Biol.* **18**: 297–313.

Crow, J.F. & Kimura, M. 1970. *An Introduction to Population Genetics Theory*. Harper and Row, New York.

Dieckmann, U. & Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* **34**: 579–612.

Diekmann, O., Gyllenberg, M. & Metz, J.A.J. 2003. Steady state analysis of structured population models. *Theor. Pop. Biol.* **63**: 309–338.

Durinx, M. & Metz, J.A.J. 2005. Multi-type branching processes and adaptive dynamics of structured populations, Section 7.8. In: *Branching Processes in Biology: Variation, Growth and Extinction* (P. Haccou, P. Jagers & V. Vatutin, eds), Cambridge University Press, Cambridge.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford.

Galis, F. & Metz, J.A.J. 2001. Testing the vulnerability of the phylotypic stage: on modularity and evolutionary conservation. *J. Exp. Zool. (Mol. Dev. Evol.)* **291**: 195–204.

Galis, F. & Metz, J.A.J. 2003. Anti-cancer selection as a source of developmental and evolutionary constraints. *Bioessays* **25**: 1035–1039.

Galis, F., van Alphen, J.J.M. & Metz, J.A.J. 2001. Why do we have five fingers? The evolutionary constraint on digit numbers. *TREE* **16**: 637–646.

Galis, F., van Dooren, T. & Metz, J.A.J. 2002. Conservation of the segmented germband stage: modularity and robustness or pleiotropy and stabilizing selection? *TIG* **18**: 504–509.

Geritz, S.A.H. 2004. Resident-invader dynamics and the coexistence of similar strategies. *J. Math. Biol.*, in press.

Geritz, S.A.H., Gyllenberg, M., Jacobs, F.J.A. & Parvinen, K. 2002. Invasion dynamics and attractor inheritance. *J. Math. Biol.* **44**: 548–560.

Geritz, S.A.H., Kisdi, É., Meszéna, G. & Metz, J.A.J. 2004. Adaptive dynamics of speciation: ecological underpinnings. In: *Adaptive Speciation* (U. Dieckmann, J. A. J. Metz, M. Doebeli & D. Tautz, eds), pp. 54–75. Cambridge University Press, Cambridge.

Gyllenberg, M., Jacobs, F.J.A. & Metz, J.A.J. 2003. On the concept of attractor in community-dynamical processes II: The case of structured populations. *J. Math. Biol.* **47**: 235–248.

Jacobs, F.J.A. & Metz, J.A.J. 2003. On the concept of attractor in community-dynamical processes I: The case of unstructured populations. *J. Math. Biol.* **47**: 222–234.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**: 314–334.

Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* **63**: 607–615.

Matsuda, H., 1985. Evolutionarily stable strategies for predator switching. *J. Theor. Biol.* **115**: 351–366.

Metz, J.A.J., in press. Invasion fitness, canonical equations, and global invasibility criteria for Mendelian populations. In: *Elements of Adaptive Dynamics* (U. Dieckmann & J. A. J. Metz, eds), Cambridge University Press, Cambridge.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. & van Heerwaarden, J.S. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems* (S. J. van Strien & S. M. Verduyn Lunel, eds), pp. 183–231, North-Holland, Amsterdam.

Metz, J.A.J. & McCune, A.R. 2004. Box 18.2: Predictions from the changing geometry of fitness landscapes. In: *Adaptive Speciation* (U. Dieckmann, J. A. J. Metz, M. Doebeli & D. Tautz, eds), pp. 372–373. Cambridge University Press, Cambridge.

Rice, S.H. 1990. A geometric model for the evolution of development. *J. Theor. Biol.* **143**: 319–342.

van Tienderen, P.H. & de Jong, G. 1986. Sex-ratio under the haystack model – polymorphism may occur. *J. Theor. Biol.* **122**: 69–81.

Waxman, D. & Gavrilets, S. 2005. 20 Questions on adaptive dynamics. *J. Evol. Biol.* **18**: 1139–1154.

Wright, S. 1937a. The distribution of gene frequencies in populations. *Science* **85**: 504.

Wright, S. 1937b. The distribution of gene frequencies in populations. *PNAS* **23**: 307–320.