

Only the combination of mathematics and agent-based simulations can leverage the full potential of evolutionary modeling

Comment on “Evolutionary game theory using agent-based methods”
by C. Adami, J. Schossau and A. Hintze

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A few years ago, the famous computer scientist William H. Press was interested in finding all stable strategies for the iterated prisoner’s dilemma, a highly influential model for the evolution of cooperation among self-interested individuals [1]. He decided to devise an algorithm for this task (which is more difficult than it may sound – after all, the iterated prisoner’s dilemma allows for infinitely many strategies). However, for particular points in the strategy space, his computer program always crashed. There is a simple cure for such problems – by making the natural additional assumption that players sometimes commit errors when implementing their strategies, one can often avoid such crashes, as many other authors did before [2]. But Press got curious. He noted that the strategies that caused the problem all lay on a plane in the respective strategy space. Press presented his results to his friend, the mathematician and physicist Freeman Dyson, who soon discovered that for those strategies a certain determinant vanishes (which explains why these strategies are now called “zero-determinant strategies”, or “ZD strategies”). While others would have been just satisfied that the cause of the program crashes had been resolved, Press and Dyson went one step further. They realized that ZD strategies are interesting on their own right. Some of the ZD strategies could be used to enforce a particular payoff upon the opponent (so-called “equalizer strategies” [3]). Others could be used to systematically outperform the opponent (so-called “extortionate strategies”). In a remarkable article [4], Press and Dyson showed how simple arguments borrowed from linear algebra can open the door to a beautiful and largely unexplored world, the world of ZD strategies [5–7]. For those who use agent-based simulations only, this entire world would have remained invisible – the space of ZD strategies has measure zero within the space of all possible strategies for the iterated prisoner’s dilemma. The discovery of ZD strategies thus illustrates that mathematics may lead to insights that are inaccessible to computer simulations alone.

In their review [8], Adami, Schossau & Hintze highlight several examples which illustrate the converse observation: “agent-based methods can predict evolutionary outcomes where purely mathematical treatments cannot tread”. Mathematical models, they argue, are often limited as they rest on many simplifying assumptions. For example, the replicator equation, which is arguably the most commonly applied dynamics to model the evolution of strategies, presumes an infinite well-mixed population, no mutations, and a finite set of feasible strategies. However, the classical replicator equation has been formulated almost 40 years ago [9]. Since then, much research has been devoted to derive mathematical models that build upon the replicator dynamics, but do not face the above restrictions. For example, to capture the effects of finite population size and population structure, one can use replicator equations with a slightly transformed payoff matrix [10, 11]. In addition, there is also an extensive literature on stochastic dynamics in finite populations [12, 13]. Some of the corresponding methods require weak selection or rare mutations. But analytical results are also available when selection is strong [14], mutation rates are arbitrary [15, 16], or when more than two players are involved in any particular interaction [17, 18]. Even the evolution in continuous strategy spaces can be captured with simple differential equations, using the framework of adaptive dynamics in infinite [19] or finite populations [20]. These models and others [21] have exactly been developed to explore situations in which mutations can lead to completely novel phenotypes that have not been present in the original population – an aspect that Adami et al. have apparently been missing in evolutionary game theory (the ‘E’ in EGT).

As a field matures, more sophisticated methods are developed or transferred from other areas. This also applies to the field of evolutionary game theory: stochastic models have been addressed in terms of coalescence theory from population genetics [22, 23], or have been analyzed using methods from quantum mechanics [24, 25]. Thus, one should not decide to focus entirely on computer simulations prematurely - mathematics may take us much further than we think now.

With these arguments, we do not wish to suggest that mathematical models are superior to agent-based simulations. On the contrary, we routinely make use of agent-based simulations ourselves, and we believe that both approaches have their own advantages. Agent-based simulations are easier to implement, they are more flexible, and they can cope with more complexity. However, in the absence of clear-cut baseline results as a reference, they can appear to become somewhat arbitrary. We thus agree with Adami et al. that “mathematical solutions [...] must be explored in order to validate the simulations.” - but simulations can only be validated if they are coded in a way that allows this kind of connection.

Mathematical approaches, on the other hand, make the underlying assumptions more explicit, and their results are often more transparent. If closed-form solutions exist, the effect of parameter changes follows immediately. But even if closed-form solutions do not exist, one may gain important qualitative results. Already simple mathematical models can often yield valuable and unexpected insights [26].

In our humble opinion, the best papers in evolutionary game theory are those in which analytical approaches and simulations complement each other. Press and Dyson have presented a beautiful example [4].

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References

- [1] http://www.edge.org/conversation/william_h_press-freeman_dyson-on-iterated-prisoners-dilemma-contains-strategies-that, retrieved September 12, 2016.
- [2] K. Sigmund. *The Calculus of Selfishness*. Princeton Univ. Press, 2010.
- [3] M. C. Boerlijst, M. A. Nowak, and K. Sigmund. Equal pay for all prisoners. *American Mathematical Monthly*, 104:303–307, 1997.
- [4] W. H. Press and F. D. Dyson. Iterated prisoner’s dilemma contains strategies that dominate any evolutionary opponent. *Proceedings of the National Academy of Sciences USA*, 109:10409–10413, 2012.
- [5] E. Akin. Stable cooperative solutions for the iterated prisoner’s dilemma. *arXiv*, page 1211.0969v2, 2013.
- [6] A. J. Stewart and J. B. Plotkin. From extortion to generosity, evolution in the iterated prisoner’s dilemma. *Proceedings of the National Academy of Sciences USA*, 110(38):15348–15353, 2013.
- [7] C. Hilbe, A. Traulsen, and K. Sigmund. Partners or rivals? Strategies for the iterated prisoner’s dilemma. *Games and Economic Behavior*, 92:41–52, 2015.
- [8] C. Adami, J. Schossau, and A. Hintze. Evolutionary game theory using agent-based methods. *Physics of Life Reviews*, this issue, 2016.
- [9] P. D. Taylor and L. Jonker. Evolutionarily stable strategies and game dynamics. *Mathematical Biosciences*, 40:145–156, 1978.
- [10] H. Ohtsuki and M. A. Nowak. The replicator equation on graphs. *Journal of Theoretical Biology*, 243:86–97, 2006.
- [11] C. Hilbe. Local replicator dynamics: A simple link between deterministic and stochastic models of evolutionary game theory. *Bulletin of Mathematical Biology*, 73:2068–2087, 2011.
- [12] M. A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg. Emergence of cooperation and evolutionary stability in finite populations. *Nature*, 428:646–650, 2004.
- [13] A. Traulsen and C. Hauert. Stochastic evolutionary game dynamics. In Heinz Georg Schuster, editor, *Reviews of Nonlinear Dynamics and Complexity*, volume II, pages 25–61. Wiley-VCH, Weinheim, 2009.
- [14] D. Fudenberg, M. A. Nowak, C. Taylor, and L. A. Imhof. Evolutionary game dynamics in finite populations with strong selection and weak mutation. *Theoretical Population Biology*, 70:352–363, 2006.
- [15] T. Antal, M. A. Nowak, and A. Traulsen. Strategy abundance in 2×2 games for arbitrary mutation rates. *Journal of Theoretical Biology*, 257:340–344, 2009.
- [16] T. Antal, A. Traulsen, H. Ohtsuki, C. E. Tarnita, and M. A. Nowak. Mutation-selection equilibrium in games with multiple strategies. *Journal of Theoretical Biology*, 258:614–622, 2009.
- [17] C. S. Gokhale and A. Traulsen. Evolutionary games in the multiverse. *Proceedings of the National Academy of Sciences USA*, 107:5500–5504, 2010.

- [18] J. Peña, B. Wu, and A. Traulsen. Ordering structured populations in multiplayer cooperation games. *Journal of The Royal Society Interface*, 13(114):20150881, 2016.
- [19] S. A. H. Geritz, J. A. J. Metz, É. Kisdi, and G. Meszéna. Dynamics of adaptation and evolutionary branching. *Physical Review Letters*, 78(10):2024–2027, 1997.
- [20] L. A. Imhof and M. A. Nowak. Stochastic evolutionary dynamics of direct reciprocity. *Proceedings of the Royal Society B*, 277:463–468, 2010.
- [21] W. Huang, B. Haubold, C. Hauert, and A. Traulsen. Emergence of stable polymorphism driven by evolutionary games between mutants. *Nature Communications*, 3:919, 2012.
- [22] S. Lessard and V. Ladret. The probability of fixation of a single mutant in an exchangeable selection model. *Journal of Mathematical Biology*, 54:721–744, 2007.
- [23] S. Lessard. Effective game matrix and inclusive payoff in group-structured populations. *Dynamic Games and Applications*, 1:301–318, 2011.
- [24] M. Mobilia and M. Assaf. Fixation in evolutionary games under non-vanishing selection. *Europhysics Letters*, 91:10002, 2010.
- [25] A. J. Black, A. Traulsen, and T. Galla. Mixing times in evolutionary games. *Physical Review Letters*, 109:028101, 2012.
- [26] M. Abou Chakra, C. Hilbe, and A. Traulsen. Plastic behaviors in hosts promote the emergence of retaliatory parasites. *Scientific Reports*, 4:4251, 2014.