

Biological markets: a catalyst for the major transitions?

Steve Phelps

August 22, 2010

Abstract

The major transitions of evolution required the emergence cooperation amongst the lower-levels of selection. Many mathematical models have uncovered sufficient conditions for the evolution of cooperation amongst selfish agents but within this framework there are as many plausible scenarios which lead to cooperative outcomes as there scenarios in which defection prospers. A new approach to explaining reciprocity appeals to the same mechanisms which have systematically enabled an explosion of reciprocity and welfare in human societies, viz. markets. The field of biological markets conjectures that Adam Smith's "invisible hand" is a universal phenomenon of nature rather than a parochial artefact of human societies. In this paper I review this field and speculate how an understanding of the role of market interactions in nature can explain the major transitions in evolution and the corresponding explosive increase in the complexity of life.

1 Introduction

One of the puzzles of evolutionary biology is that the complexity we observe in nature cannot always be explained solely by natural selection operating at the level of individual genes. For most of our planet's history, life consisted of simple single-celled organisms and it is only relatively recently that a diverse range of more complex and specialized phenotypes emerged. In early evolutionary history, genes themselves were not the original replicators. Rather, the intricate machinery for replicating strands of DNA itself evolved from more primitive systems of molecules that were able to self-replicate in the absence of enzymes [Maynard Smith, 1993, p. 113]. Complexity in nature emerged from a series of such "major transitions" in the units of selection: genes cooperated to form regulatory networks; similarly cells emerged from networks, multi-cellular organisms from cells and societies from organisms [Maynard Smith and Szathmary, 1995].

There is an *economic* aspect to these major transitions from lower-level to higher-level selection:

“These transitions in the units of selection share two common themes: the emergence of cooperation among the lower-level units in the functioning of the new higher-level unit, and the regulation of conflict among the lower-level units.” [Michod, 1999, p. 7]

Thus we exchange one puzzle for another: if the major transitions require the evolution of cooperation between lower-level selfish replicators, and we wish to explain how the transition to higher levels of selection is *systematic*, as opposed rather than merely serendipitous, then we need to explain how cooperative strategies can systematically evolve in populations of selfish agents. A great deal of research has uncovered sufficient conditions for cooperative outcomes. However, although there are many stylised scenarios in which cooperation can be shown to stable, there are equally many in which defection prospers.

A new approach to explaining reciprocity in nature appeals to one of the mechanisms that enable reciprocity in human societies, viz. *markets* [Henzi and Barrett, 2002]. The central insight is that just as trade can give rise to specialisation and mutual benefit (“efficiency”) in our own species, the same principles apply to interactions in other species. The hypothesis is that this “invisible hand” is a universal phenomenon of nature rather than a parochial artefact applying only to humans. For example, we might gain insights from viewing fruit as a payment for a service: flora donate energy to fauna in the form of fructose and in return fauna disperse seed [Bronstein, 2001]. The description of this mutualism in terms of trade offers more than a descriptive analogy since it allows us to make predictions contingent on economic theory. For example, we should expect payments (fructose yields) to reflect conditions of supply and demand: the fructose to seed ratio should be higher when there are fewer fruit-eating fauna and lower when there are greater numbers of fruit-bearing flora [Hoeksema and Schwartz, 2001, p. 182].

If the invisible hand is indeed a universal phenomenon of nature, it provides a powerful explanation for the major transitions: for example, biodiversity arises from speciation, which I shall argue arises from economic incentives to specialise.

2 The Energy Economy

Energy plays a central role in biology. Organisms cannot reproduce without sufficient energy reserves, thus an organism’s ability to acquire energy through foraging, predation or photosynthesis is a key determinant of its fitness. If fitness increases with energy, then genes will seek strategies that maximise energy; thus the central paradigm of behavioural ecology is optimal foraging theory which attempts to explain animal behaviour in terms of energy maximisation.

In economics, the notion of fitness is replaced with the notion of *utility*, which agents attempt to maximise. Since utility embodies preferences for states of the world which can often be purchased using cash, economic actors can typically increase their utility by increasing their wealth. This is because cash is a special commodity called a numéraire; it is meaningful to compare the value of two

commodities by comparing how many units of a reference commodity, that is the numéraire, each commodity will be exchanged for in the marketplace. Since cash is universally exchanged for almost any commodity it becomes a natural numéraire. However, it is not always appropriate to compare value in terms of cash [Benninga et al., 2002]. Similarly, although energy yield and its statistical properties play a central role in determining fitness in biology, energy is not the *sole* numéraire in biological markets. For example, Barrett et al. [1999] find that grooming effort is a natural “currency” which explains many observed interactions in baboon societies. Nevertheless it is instructive to focus on the role of energy as a numéraire because of its universal role across different species.

It is easier to observe wealth than it is to observe utility, hence monetary incentives are the staple of behavioural economics experiments just as calorific values are used in optimal foraging studies.

Just as money can be transferred between participants in a market, energy can be transferred between organisms of the same or different species in the form of food. At first glance, it seems that most such interactions in nature cause a reduction in fitness, in which case we can think of the donor as being exploited by the recipient (eg when losing nutrients or flesh to a parasite or predator)¹.

However, the transfer of energy may also be of some fitness *benefit* to the originator of the transaction (eg a mother bird feeding chicks or a fruit tree feeding birds), in which case we can think of it as analogous to a payment.

Thus energy can be *traded*. It can also be stored (via fat deposits or through caching [Pravosudov and Grubb, 1997]), invested (via foraging or predation) or consumed (via reproduction). Fat deposits are analogous to buying “risk-free” financial instruments such as a bonds. Foraging and predation are analogous to investment: energy is spent on short-term activities which yield higher energy payoffs in the future. Investment can be *risky* which can lead to hedging strategies (we return to this in Section 2.2). Finally, just as wealth is a means to an end (utility) in economics, energy is a means to fitness in biology: once sufficient energy reserves have been stockpiled they can be cashed in for fitness through the expensive process of reproduction.

A physicist might object to this analogy between energy and money since energy is conserved whereas money it seems is not: money can be invested, economies can inflate. However, this apparent liquidity is an illusion: the total cash available to an economy is capped by the money supply, just as the total energy available to an ecosystem is capped by supply of energy from the sun. Just as the money supply is variable, the total solar energy available to an ecosystem changes with climate. Moreover, just as the cost of money (borrowing) is determined by an economy’s financial infrastructure, ecosystems can vary in the efficiency with which they extract solar energy; plants can improve their

¹Appropriation of wealth in economics takes several forms. When it is illegal it is called fraud or theft. When it is legal it is called rent-seeking. Since there is no governance in nature, appropriation of energy falls into the former category. However it is interesting to note that the latter form has persisted throughout human economic history [Kay, 2004] and thus misappropriation is common to both biological and artificial markets.

ability to photosynthesise which affects the energy available to other species higher up the food chain. Despite the conservation of energy, there is still room for *growth* within in an ecosystem within the constraints provided by sunlight.

This perspective on the role of energy in evolution has been developed into the field of *Thermoeconomics*:

“*Free-loading* – better known as predation – may also be a (relatively) low-cost way to obtain available energy, and this alternative strategy is also likely to have developed early on in the evolution of the prokaryotes. However, a major evolutionary breakthrough occurred when a new class of predators (heterotrophs) developed the ability to utilize an accumulating biological waste product (oxygen) to bypass the rigors of photosynthesis and extract energy directly from the biomass of the so-called *autotrophs* (e.g., plants and grasses) using oxidative combustion. This represented a significantly more economical biotechnology. Equally important, it freed the heterotrophs from the need to sit in the sun all day and remain connected to an array of solar panels. However, as Fenchel and Finley (1994) point out, these increasingly complex forms of energy capture and metabolism were the result of synergistic functional developments that produced adaptive *economic* advantages, and not thermodynamic *instabilities, fluctuations, or bifurcations*.” [Corning, 2002, p. 17]

2.1 Secure payment systems in ecology

The concept of the so-called “free-market” is almost always an idealisation. In practice, markets rely heavily on contractual regulation and enforcement to, for example, prevent one party involved in a transaction from renegeing on the other. Real markets are underpinned by *reliable* mechanisms for transacting goods and currency in order to mitigate counter-party risk. Given that there is no “government” in an ecology, how could a biological market ever get off the ground? It seems that we need some way of securing payments in nature.

One possible work-around is that trade occurs selectively with counter-parties who have been trustworthy in the past using a strategy similar to tit-for-tat [Axelrod, 1997]. However, Roberts and Sherratt [1998] noted that *tit-for-tat* like strategies are rarely observed in ecological field studies.

We can gain some insight into the payments issue by examining human markets for illegal goods such as drugs (“black markets”) in which the participants have no legal recourse in the event of a counter-party renegeing. One common strategy for mitigating counter-party risk in such markets is to perform transactions *incrementally*:

“Consider the situation of two dealers who are about to trade among themselves a large amount of heroin for a large amount of money. How is it possible to ensure that the one who offers the heroin does not turn around with the million dollars in his hands before handing out the heroin? One

way is to parcel both money and heroin and exchange small portions. If one dealer does not get his portion, he will stop trading and this is why the other has to continue being fair.” [Noë et al., 2001, p. 16]

Friedman and Hammerstein [1991] analyse the mating behavior of a species of fish: *hypoplectrus nigricans* or “black hamlet”. These fish are hermaphrodites, individual Hamlets produce both eggs and sperm. They mate in pairs and take alternative turns to fertilise a small number of eggs provided by their partner. Friedman and Hammerstein conjecture that this is a form of *trading*; the ratio of sperm to eggs in the general population is so large that it is profitable in terms of reproductive success to “buy” unfertilized eggs in return for left-over sperm. The slow incremental nature of the exchange serves two economic purposes: i) as a hedge against counter-party risk; and ii) as a means of reducing the “market-impact” from flooding the market with an excess supply of perishable goods which would reduce the “price”. The latter strategy is similar to volume-participation algorithms for executing large trades of financial assets [Bialkowski et al., 2008].

Incremental exchange has been proposed a general model for explaining the emergence of trust in the absence of enforced contracts [Kurzban et al., 2008]. In an evolutionary context Roberts and Sherratt [1998] studied a simulated evolutionary tournament of a variant of the prisoner’s dilemma game that allows for incremental levels of cooperation, and found that a strategy *raise-the-stakes* was an evolutionary stable outcome. In later work Roberts and Renwick [2003] studied human subjects and found that they used a strategy similar to *raise-the-stakes*. This strategy starts off with a small level of cooperation and then rises to maximal cooperation dependent on the other player’s level of cooperation in previous rounds. The behavior of this strategy is qualitatively consistent with the self-reported behavior of human subjects in longitudinal studies of friendship development as reported by Hays [1985].

An alternative approach to the problem of secure payments is to “lock” the resource being traded in such a way that the only way to open it is to reciprocate. For example, if we view the fructose in fruit as a payment made by flora to fauna in return for seed dispersal, we see that is is very difficult (i.e. costly) for the frugivore to consume the fructose without performing the dispersal service, since it would become literally a “sitting duck” for predators. By encapsulating the seed within the fructose, the co-evolution between frugivore and plant has resulted in the evolution of a secure payment system.

2.2 Is Nature Risk-Sensitive?

In a market, an individual’s circumstances and preferences determine the quantitative relationship between their wealth and utility, which is not always linear. In this case, in a stochastic environment agents will be sensitive not only to the expected value of their wealth, but also the variance in possible outcomes: agents will be sensitive to *risk*. For example, if the relationship is concave then the agent is said to be *risk-averse* and may attempt to reduce risk through hedging.

Similarly, in an ecological context the specifics of a particular phenotype and niche will determine fitness yields as a function of energy. If this function is non-linear then we should predict *risk-sensitive* strategies for behaviours such as foraging [Harder and Real, 1987, Bateson, 2002, Bednekoff, 1996] which mitigate against the risk of extreme events that would cause starvation or extinction.

Markets allow agents to reduce risk through diversification. A carefully constructed *portfolio* of assets yields a lower risk than any of the individual assets provided that the returns on investment are negatively correlated between assets. Similarly a gene operating in a risk-sensitive niche can invest in a portfolio of strategies in order to reduce variance in energy yield [Real, 1980] and hence reduce the risk of starvation.

2.3 The efficient ecosystems hypothesis

In order to understand mutualisms in nature arising from trade we need to understand the process through which “prices” are determined. In economics the corresponding theory is called *microeconomics*, which studies how scarce resources are allocated to utility-maximising agents and the conditions under which such allocations are Pareto-efficient².

It is interesting to consider whether ecosystems are “efficient” in a similar sense. For example, do ecosystems maximise their total potential fitness, or could one or more species gain additional fitness (through trade) without making another species worse off (through predation)? This suggests a new way of looking at the concept of *carrying capacity*, since we can ask whether an ecosystem’s carrying capacity could be improved by intra-species trade. The ratio of the actual to maximal carrying capacity would determine the current efficiency of the ecosystem.

The key concept in economics for understanding how efficient prices are determined is an *auction*³. Agents submit *signals* indicating the level of their valuations for a scarce resource which they either want to buy or sell and the auctioneer awards the resource to the agent(s) who value it the most. However, in the absence of payments such a mechanism is vulnerable to manipulation since agents can mis-report their valuation in order to greedily consume resources that would be more beneficial to other agents with higher actual valuations. In the vernacular of game theory such a mechanism does not necessarily incentivise *honest signalling*. Once we force agents to back up their value claims with hard cash, however, it becomes possible to design mechanisms that are *incentive-compatible*; that is, mechanisms in which the best strategy is to submit a truthful signal with respect to each agent’s actual valuation. The signals become *bids*: signals of valuations with a corresponding commitment to pay a specified price on completion of a transaction. By reasoning carefully we can set up the rules of the auction in such a way that the dominant strategy is to bid truthfully. In economics this is called *mechanism design* [Phelps, 2007].

²That is, no agent can be made better off without making another agent worse off.

³See the discussion of Walrasian tâtonnement in [Walras, 2005, p. xxix].

We observe similar signalling problems in nature [Johnstone, 1997]. For example, babbler fledglings cry loudly when hungry. The crying is a signal to their mother of their demand for a scarce resource, but how does the mother know that this is a truthful signal, and that the crying fledgling is genuinely in more need of nourishment than its siblings? Zahavi and Zahavi [1997]⁴ conjecture that this signal bears a corresponding cost (the danger of the cry attracting predators) and that truthful signalling is an ESS of a strategic signalling game between parent and offspring precisely because talk is not cheap; the marginal benefits from receiving food when not hungry do not outweigh the costs of attracting predators. Thus if signals have an associated cost or *handicap* then truthful signalling can co-evolve between self-interested parties. Similarly we can think of the payments attached to bids in a conventional auction as “handicaps” which incentivise honest signalling in human marketplaces [Phelps, 2007, p. 25].

2.4 Speciation and Specialisation

One of the big puzzles of evolutionary biology is the cause of increasing complexity and biodiversity in the history of evolution. It is only following the relatively recent Cambrian explosion that we see a diverse range of complex species in the fossil record. We observe a similar explosion of complexity in economic history: De Long [1998] estimates world GDP from One Million years B.C. to the present day and finds an explosion of exponential growth coinciding with the industrial revolution. Is there a common principle underlying the explosion of complexity in both economic and biological history?

There are two main drives towards diversification and hence heterogeneity in markets: (i) hedging leading an individual investor to diversify their investments and (ii) division of labour leading different individuals to specialise in diverse directions.

We have already discussed risk-sensitivity resulting and hedging: a diverse portfolio of investments has a smaller variance in returns than any single asset in the portfolio. Similarly a diverse portfolio of, e.g. foraging strategies can be used to reduce the risk of famine.

On the other hand, trade between individuals can lead to a pressure in the opposite direction, i.e. *specialisation*, as illustrated by Adam Smith’s description of a pin factory:

“One man could scarce, perhaps, with his utmost industry, make one pin in a day, and certainly could not make twenty. But in the way in which this business is now carried on, not only the whole work is a peculiar trade, but it is divided into a number of branches, of which the greater part are likewise peculiar trades. One man draws out the wire, another straightens it, a third cuts it, a fourth points it, a fifth grinds it at the top for receiving the head.”

⁴p. 120

Specialisation of this kind leads to *diversity* at the level of the system as a whole because individuals specialise in *different* activities. We might expect a similar driving force behind biodiversity in nature [Houthakker, 1956].

Schwartz and Hoeksema [1998] provide a hypothetical example of trade between a species of vascular plant and a mycorrhizal fungus. Each species requires both carbon and phosphorous for growth but they have varying efficiency with which they can fix each element. Despite the fact that the plant is more efficient at fixing both elements in absolute terms (the rate of fixation expressed as mass per unit time), the principle of *comparative advantage* means that both species of plant would be better off in terms of growth rates if they were to each specialise in fixing a single element and obtain their recommended daily intake of the missing element by trading any surplus. This strategy maximises growth for each individual species because neither species has an advantage in the *relative* cost of extracting both elements since there is an implicit opportunity cost: increasing production of one element means foregoing production of the other.

In this hypothetical example the ecosystem as a whole can increase its carrying capacity by exploiting *gains from trade*. Moreover, this trade is incentive-compatible: each individual species is maximising its own local fitness without regard for the welfare of the other; meanwhile the “invisible hand” maximises the global carrying capacity.

3 Empirical Evidence

Thus far I have surveyed literature which makes a convincing case that biological markets are a plausible framework for understanding many mutualisms in nature, but to what extent do these models make testable predictions, and are there any that are falsified by empirical evidence? Hoeksema and Schwartz [2003] make some highly specific predictions contingent on the comparative advantage explanation for plant-fungus mutualism. Kiers and Van Der Heijden [2006] weigh the empirical evidence for and against this and alternative hypotheses which explain these mutualisms. Whilst they find some evidence in support of the comparative advantage explanation they are not able to conclusively falsify alternative explanations.

3.1 Artificial Life Models

4 Conclusion

References

- R. Axelrod. *The Complexity of Cooperation: Agent-based Models of Competition and Collaboration*. Princeton University Press, 1997.
- L. Barrett, S. P. Henzi, T. Weingrill, J. E. Lycett, and R. A. Hill. Market forces predict grooming reciprocity in female baboons. *Proceedings of*

- the Royal Society B: Biological Sciences*, 266(1420):665, April 1999. doi: 10.1098/rspb.1999.0687.
- M. Bateson. Recent advances in our understanding of risk-sensitive foraging preferences. In *Proceedings of the Nutrition Society*, volume 61, pages 1–8, 2002. doi: doi:10.1079/PNS2002181.
- P. A. Bednekoff. Risk-sensitive foraging, fitness, and life histories: Where does reproduction fit into the big picture. *American Zoology*, 36:471–483, 1996.
- S. Benninga, T. Björk, and Z. Winer. On the use of numeraires in option pricing. *The Journal of Derivatives*, 10(2):43–58, 2002.
- J. Bialkowski, S. Darolles, and G. Lefol. Improving VWAP strategies: A dynamic volume approach. *Journal of Banking & Finance*, 32(9):1709–1722, September 2008. ISSN 03784266. doi: 10.1016/j.jbankfin.2007.09.023.
- J. L. Bronstein. The costs of mutualism. *American Zoologist*, 41(4):825–839, August 2001. doi: 10.1093/icb/41.4.825.
- P. A. Corning. Thermoconomics: Beyond the second law. *Journal of Bioeconomics*, 4(1):57–88, January 2002. ISSN 13876996. doi: 10.1023/A:1020633317271.
- J. B. De Long. Estimating World GDP, One Million B.C. to Present, 1998. URL http://www.j-bradford-delong.net/TCEH/1998.Draft/World.GDP/Estimating_World.GDP.html.
- J. Friedman and P. Hammerstein. To trade, or not to trade; that is the question. In *Game Equilibrium Models I: Evolution and Game Dynamics*, pages 257–275. Springer-Verlag, 1991.
- Lawrence D. Harder and Leslie A. Real. Why are bumble bees risk averse? *Ecology*, 68(4):1104–1108, 1987. ISSN 00129658. doi: 10.2307/1938384.
- R. B. Hays. A longitudinal study of friendship development. *Journal of Personality and Social Psychology*, 48(4):909–924, 1985.
- S. P. Henzi and L. Barrett. Infants as a commodity in a baboon market. *Animal Behaviour*, 63:915–921, 2002. doi: doi:10.1006/anbe.2001.1986.
- J. D. Hoeksema and M. W. Schwartz. Interspecific mutualisms as biological markets. In *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*, chapter 8, pages 173–184. 2001.
- J. D. Hoeksema and M. W. Schwartz. Expanding comparativeadvantage biological market models: contingency of mutualism on partner’s resource requirements and acquisition tradeoffs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270(1518):913–919, May 2003. doi: 10.1098/rspb.2002.2312.

- H. S. Houthakker. Economics and biology: Specialization and speciation. *Kyklos*, 9(2):181–189, 1956. ISSN 1467-6435. doi: 10.1111/j.1467-6435.1956.tb02716.x.
- R. A. Johnstone. The evolution of animal signals. In J. R. Krebs and N. B. Davies, editors, *Behavioural Ecology*, chapter 7, pages 155–178. Blackwell, 1997.
- J. Kay. *The Truth About Markets : Why Some Countries are Rich and Others Remain Poor*. Penguin, New Ed edition, 2004.
- E. T. Kiers and M. G. A. Van Der Heijden. Mutualistic stability in the arbuscular mycorrhizal symbiosis: exploring hypotheses of evolutionary cooperation. *Ecology*, 87(7):1627–1636, 2006.
- Robert Kurzban, Mary Rigdon, and Bart Wilson. Incremental approaches to establishing trust. *Experimental Economics*, 11(4):370–389, December 2008. ISSN 1386-4157. doi: 10.1007/s10683-007-9173-1.
- J. Maynard Smith. *The Theory of Evolution*. Cambridge University Press, 1993.
- J. Maynard Smith and E. Szathmáry. *The Major Transitions In Evolution*. Oxford University Press, 1995.
- R. E. Michod. *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton University Press, 1999.
- R. Noë, Hooff, and P. Hammerstein, editors. *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*. Cambridge University Press, 2001.
- S. Phelps. *Evolutionary mechanism design*. PhD thesis, School of Computer Science, 2007.
- V. V. Pravosudov and T. C. Grubb. Management of fat reserves and food caches in tufted titmice (*parus bicolor*) in relation to unpredictable food supply. *Behavioral Ecology*, 8(3):332–339, May 1997. doi: 10.1093/beheco/8.3.332.
- L. A. Real. Fitness, uncertainty, and the role of diversification in evolution and behavior. *The American Naturalist*, 115(5):623–638, May 1980.
- G. Roberts and J. S. Renwick. The development of cooperative relationships: an experiment. *Proceedings of the Royal Society*, 270:2279–2283, 2003.
- G. Roberts and T. N. Sherratt. Development of cooperative relationships through increasing investment. *Nature*, 394:175–179, 1998.
- M. W. Schwartz and J. D. Hoeksema. Specialization and resource trade: biological markets as a model of mutualisms. *Ecology*, 79(3):1029–1038, April 1998.

L. Walras. *Studies in Applied Economics: Theory of the Production of Social Wealth*, volume 1. Routledge, London, 2005.

A. Zahavi and A. Zavahi. *The Handicap Principle: A Missing Piece of Darwin's Puzzle*. Oxford University Press, 1997.