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ECONOMIC DRIVERS OF BIOLOGICAL COMPLEXITY

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Abstract. The complexity that we observe in nature can often be explained in terms of cooperative behavior. For example, the major transitions of evolution required the emergence of cooperation among the lower-level units of selection, which led to specialization through division-of-labor ultimately resulting in spontaneous order. There are two aspects to address explaining how such cooperation is sustained: how free-riders are prevented from free-riding on the benefits of cooperative tasks, and just as importantly, how those social benefits arise. We review these problems from an economic perspective, and highlight how ideas from economics can help us to better understand how the benefits of social interactions arise, how they are sustained, and how they affect the underlying social dilemmas.

The complexity we observe in nature cannot always be explained solely by natural selection operating at the level of individual genes. Rather, biological complexity arose in evolution through successive transitions whereby small individual units of replication were subsumed into larger units [Maynard Smith and Szathmáry, 1995, Bourke, 2011]; molecules became DNA, which formed into networks, which formed into cells, which became eukaryotic, which then formed into multi-cellular organisms, and finally societies. All of these transitions can be described as *social* evolution because the survival success of the larger individual whether a cell, a mammal, or a society depends on the harmonious *cooperation* of its component units [Bourke, 2011][1].

Hence, one of the key goals in evolutionary biology is to explain how cooperation is achieved among these units and how conflict is governed. Cooperation occurs when one individual pays a cost which results in a benefit to another [Nowak, 2006]. A defector, on the other hand, forgoes the cost and provides no benefit. Conflict arises because, a priori, we should expect natural selection to drive out cooperators in favor of defectors. Thus much recent work in evolutionary biology attempts to explain the prevalence of cooperation in the face of selfish units such as genes.

Ultimately, we argue that this is an economic issue, and in this paper we highlight the economic underpinnings of biological interactions that lead to cooperation and biological complexity. For example, many conflicts in nature can be characterized as principal-agent problems [Grossman and Hart, 2010], or free-rider problems [Hardin, 1968]. In a principal-agent relationship, conflicts can arise because information asymmetries enable exploitation of the principal by the agent, whereas in the case of the free-rider problem non-cooperative agents can benefit from a public-good without contributing towards the cost. In human societies, markets have been proposed to solve each of these problems by introducing property-rights [De Alessi, 1980], payments [Berhold, 1971, Smith, 1981] or sanctions to align incentives toward cooperative outcomes; consider, for example, emissions-trading as a mechanism of managing the atmosphere as a

[1]The major transitions in evolution were later subdivided into egalitarian and fraternal, the former applying to non-related cooperation and the latter to kin relations [Queller, 1997, Bourke, 2011]. This dichotomy has implications for how cooperation plays out on the levels [Bourke, 2011]: for example, fraternal entities are more likely to comprise division into reproducing and non-reproducing units in order to promote inclusive fitness.

common-pool resource [Tietenberg, 1985]. Given that similar problems occur throughout biology [Turner and Chao, 1999, Weyl et al., 2010], one can ask if there is an biological analogy of these economic concepts that could bootstrap systemic large-scale cooperation in nature.

Analogies are an integral tool in scientific explanation, and allow us to make inferences when two phenomena have parallel mechanisms but there is more data about one than the other [Hesse, 1974]. Analogies between biology and economics are not new, going right back to Darwin who himself was probably somewhat influenced by Malthus and Adam Smith [Armstrong, 2007]. Congruent with this has been the development of biological markets theory [Noë and Hammerstein, 1995, Noë et al., 2001, Hammerstein, 2003b]: a framework which emphasizes the importance of competition in partner-choice and exchange of naturally-occurring commodities in behavioral ecology. In other words, biological market theory attempts to explain interactions between non-human animals using economic principles such as supply and demand and market equilibrium. More recently Strassmann and Queller [2014] apply the concept of "property" to biology, reviewing many examples where organisms can thrive by delimiting resources (those external to the body) for private consumption, restricting access to others: a form of "privatization" (analogous to human property) of theoretical interest because it is one solution to the tragedy of the commons. Examples (which can be on the individual or group level) include animal territoriality (protecting a spatial area or food source), and methods of privatizing can include defense (chemically or behaviorally), carrying the resource around, mate guarding, social exclusion, creating a fortress, or concealing the resource [Strassmann and Queller, 2014].

In this paper, we discuss the economic pre-requisites for large-scale cooperation and division-of-labor, and their implications not only for biodiversity in nature, but also more generally for complex-adaptive systems. Our key contribution is to highlight that economic ideas such as *the efficiency* of a market can help to explain not only how free-riding is prevented, but also to explain how the benefits of cooperative behavior are generated — the so-called "second-problem" of cooperative behavior [Calcott, 2008]. These problems are highly related, because a greater generation of benefit can, in turn, lead to a decrease in free-riding, as the temptation to defect is reduced.

In Section 1 we give an overview of economic ideas that have been adopted by biologists, and how they relate to cooperative behavior and complexity in nature. One of the most important economic ideas in explaining biological complexity is division of labor. In Section 2 we discuss how division of labor can arise from trade via the principle of comparative advantage, and discuss the possibility of trade arising in naturalistic settings. In Section 3 we discuss the role of energy in understanding how costs and benefits are transfered in competitive or mutualistic interactions, and how these might be considered as analogs of payments or sanctions. Human markets typically require outside institutional enforcement of contracts in order to make payments binding. In Section 4 we discuss how analogs of trade can arise without strong institutional regulation. Once it is understood that interactions between species can incorporate payments and sanctions, the distinction between strictly mutalistic or strictly competitive interactions is blurred. In Section 5 we discuss how this can result in social benefits at the level of ecosystems. Human markets are not always efficient due to the possibility of market-failure arising from, e.g. strategic bidding in oligopoly and monopoly settings. In Section 6 we discuss microeconomics in an ecological context, and the role of signaling in mating markets. Finally we conclude in Section 7.

1. Economics in nature

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 *systemic*, rather than exceptional, 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 altruism in nature. Hamilton [1963] showed how altruistic behaviour could evolve through the mechanism of kin selection. Trivers [1971] widened the pre-requisites of altruism by postulating that, in addition to kin selection, reciprocity among non-kin could be driven by strategies based on conditional reciprocity; e.g. cooperating with those who are themselves altruistic. Many subsequent models show that various forms of conditional reciprocity can bootstrap cooperation even in the absence of kin selection (e.g. [Axelrod, 1997, Nowak and Sigmund, 1998, 2005]).

There are two key problems that need to be addressed in order to explain cooperative behavior: (i) understanding the conditions under which potential cheaters be prevented from free-riding on the benefits of a social interaction, and, just as importantly, (ii) understanding *how that benefit itself arises* [Calcott, 2008].

Regarding the first problem, much theoretical research has uncovered the precise pre-requisites for sustaining cooperation despite the possibility of free-riding. For example, whether or not a population fixes on cooperative as opposed to uncooperative strategies can depend on: the initial fraction of unconditional cooperators, the exact subset of possible alleles considered in the analysis (which can be chosen from an infinite space of possible strategies), the population structure (networked, island, or single population), the population size, the presence or otherwise of genetic-drift and mutation, and the payoff-structure of the underlying social dilemma (snowdrift or prisoner's dilemma) [Santos et al., 2006, Panchanathan and Boyd, 2003, Leimar and Hammerstein, 2001].

Regarding the second problem, biologists are increasingly turning to explanations of how benefits arise in human societies, viz. *markets* [Noë and Hammerstein, 1995, Noë et al., 2001, Henzi and Barrett, 2002, Hammerstein, 2003b]. The central insight is that just as trade can give rise to specialization and mutual benefit[2] in our own species, the same principles can apply to interactions in other species.

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].

Many empirical studies have successfully identified economic processes in animal behavior, which includes reciprocation (exchange of a non-storable commodity for itself), interchange (exchanging different commodities) and market value where the desirability of a commodity depends on its supply in the population. Many studies focus on grooming behavior [Hart and Hart, 1992, Henzi and Barrett, 2002, Russell and Phelps, 2013], since allogrooming forms the basis of many social behaviors in non-human animals, and like energy, the time invested in allogrooming is a fungible resource.

For example, Henzi and Barrett [2002] identified a biological market among female baboons whereby time invested in allogrooming (one baboon grooming the other, to the recipient's benefit) was exchanged for the opportunity to handle an infant baboon for a finite time (interchange). In other words, grooming was used as a medium of exchange to trade a scarce resource (access to infants). Moreover, the "market value" of

[2]In economics, this is measured as the social welfare, or allocative "efficiency", of the outcome.

each infant was inversely proportional to the number of similar infants in the group. While it may be argued that in this case, the real underlying costs and benefits cannot be directly observed, nevertheless by taking time-investments as proxies for the ultimate fitness values, a model based on supply and demand has real explanatory power, at least in over short time-horizons, and therefore the interpretation of grooming as a market payment deserves to be taken seriously [Russell and Phelps, 2013].

Allogrooming can also be exchanged for reciprocal allogrooming. The costs and benefits of this kind of interaction can be understood as a variant of a social dilemma called a donation game [Nowak and Sigmund, 2005]. In a donation game pairs of individuals interact, one of whom decides whether or not to invest in a task which incurs some cost c but results in a benefit b to the other individual which is proportional to the investment: $b = m \times c$. In the context of allogrooming, for example, the ultimate cost might be the opportunity-cost of forgoing other fitness-enhancing activities during the time invested in allogrooming another individual, and the benefit would correspond to the gains from parasite elimination and the conditioning of fur.

In such interactions, provided that the cost benefit ratio b/c is greater than one, (i.e. $m > 1$), reciprocating individuals can do better than solitary individuals, provided that one party does not cheat by accepting the benefits without providing a reciprocal investment. Accordingly, much work on the evolution of cooperation studies the conditions under which such cheating is driven out of the population, e.g. [Nowak, 2006].

In more general contexts, there is another issue to explain, which is how the benefits from social interaction arise, and the conditions under which they are maximised [Calcott, 2008] — that is, in the context of a donation game, we can ask what ecological factors contribute to higher multipliers m. This is precisely the question addressed by biological market theory, and is of crucial importance for understanding cooperative behavior, since when social surpluses are larger relative to costs, the temptation to defect is lessened, which can lead to greater cooperation. For example one of the rules introduced by Nowak [2006] for the evolution of cooperation states that cooperation can evolve through direct reciprocity when $w > c/b$ where w is the probability of encounter between the same two individuals. The first problem of cooperation resides in the left-hand side of this inequality; repeated interactions in a small well-mixed group will lead to a greater value of w, and cooperation can evolve through reciprocity directly between pairs of individuals. The second problem of cooperation resides in the right-hand side; *larger benefits* relative to costs can also lead to cooperative outcomes.

In microeconomic theory, market outcomes are often assessed as to their allocative *efficiency* and their ability to maximize social surplus despite the absence of any explicit coordination mechanism which selects efficient allocations. We argue that this is a missing piece of the biological markets puzzle, and in Section 5 we posit that by studying the efficiency of ecological interactions we can better understand the resulting complexity. Meanwhile in the following section, we review one of the most fundamental ways that cooperative behavior can result in biological complexity, viz. through division-of-labor.

2. Specialization and Division of Labor

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 well-known drives towards diversification and hence heterogeneity in markets: (i) division of labor leading different individuals to specialize in diverse directions, and (ii) hedging of risk leading an individual investor to diversify their investments. The former is one the key ideas that has been incorporated from economics into biology to explain *specialization*, as illustrated by Adam Smith's description of a pin factory [Smith, 2007, p. 15].

> "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 straights it, a third cuts it, a fourth points it, a fifth grinds it at the top for receiving the head." [Smith, 2007, p. 15]

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

Specialization and division of labour often occur within species, most notably in eusocial insects [Traniello and Rosengaus, 1997, Gautrais et al., 2002, Ferguson-Gow et al., 2014]. However, when resources can be exchanged, it is possible that biological "trade" can lead to division of labour *between* species.

In artificial economies, trade between nations can result in specialization in the production of certain resources through the principle of *comparative advantage*, which was first illustrated by Ricardo's famous example of wine verses cloth production:

> "The quantity of wine which she [Portugal] shall give in exchange for the cloth of England, is not determined by the respective quantities of labour devoted to the production of each, as it would be, if both commodities were manufactured in England, or both in Portugal.
>
> England may be so circumstanced, that to produce the cloth may require the labour of 100 men for one year; and if she attempted to make the wine, it might require the labour of 120 men for the same time. England would therefore find it her interest to import wine, and purchase to it by the exportation of cloth.
>
> To produce the wine in Portugal, might require only the labour of 80 men for one year, and to produce the cloth in the same country, might require the labour of 90 men for the same time. It would therefore be advantageous for her to export wine in exchange for cloth. This exchange might even take place, notwithstanding that the commodity imported by Portugal could be produced there with less labour than in England. Though she could make the cloth with the labour of 90 men, she would import it from a country where it required the labour of 100 men to produce it, because it would be advantageous to her rather to employ her capital in the production of wine, for which she would obtain more cloth from England, than she could produce by diverting a portion of her capital from the cultivation of vines to the manufacture of cloth.
>
> Thus England would give the produce of the labour of 100 men, for the produce of the labour of 80." [Ricardo, 1817, p. 42]

If an analog of trade can occur between species, we should expect to see similar pressures for specialization in nature. For example, Schwartz and Hoeksema [1998] and Wyatt et al. [2014] analyze the symbiosis between plants and mycorrizhizal fungus using models of trade. 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 specialize in fixing a single element and obtain their recommended daily intake of the missing element by trading any surplus. This strategy maximizes 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 these examples the ecosystem as a whole can increase in size by exploiting *gains from trade*. Moreover, this trade is incentive-compatible: each individual is maximizing its own local fitness without regard for the welfare of the other; meanwhile the "invisible hand" results in a mutually beneficially outcome.

Division of labor can eventually lead to greater cooperation between previously competing species, most famously illustrated by the endosymbiosis theory of mitochondrial evolution [Margulis, 1981]. Just as evolutionary biology discusses natural selection operating at different levels of organization, modern economic theory attempts to explain the emergence of higher-level structures. According to the neo-classical economic view the primary actors in the economy are individuals, yet clearly much trade occurs between collections of individuals such as firms. Coase [1937] argued that firms arise in order to mitigate transaction costs (e.g. the costs involved in drawing up contracts, or brokerage fees). At an even higher-level, through the process of mergers and acquisitions, previously competing firms can merge resulting in a more complex entity in order to become more efficient in Cournot-competition settings [Zedan et al., 2012]. Similarly we could think of endosymbiosis between e.g. mitochondria and cells [Sagan, 1967, Margulis, 1981] as being driven by a process to reduce transaction-costs between symbionts. This then results in an *egalitarian* transition [Queller, 1997] in the level of selection; the division of labor resulting from symbiosis in turn results in specialization within a single unit — the cell — which in turn increases its complexity.

The greatest hurdle to overcome for egalitarian transitions such as this is the regulation of conflict between unrelated individuals, which we will discuss further in Section 4. Meanwhile, as discussed above, we have seen that the possibility of exchanging resources between individuals can play an important role in the division of labor. In the next section we discuss the possibility of more general mechanisms for exchange of resources, including in the ecosystem as a whole.

3. 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 maximize energy; thus the central paradigm of behavioral ecology is optimal foraging theory which attempts to explain animal behavior in terms of energy maximization.

According to Van Valen [1976] "Energy drives evolution just as it drives physiological processes" (p. 180) and evolution can be construed as energy expansion on the species level (rather than focusing on individuals). Within this view, all competition for resources is competition for energy (e.g. food would be considered a surrogate resource because when animals compete for food, they are ultimately competing for energy) and the success of species is measurable as the success in controlling trophic energy (i.e. energy available at the trophic level of the organism; more on this below). Van Valen (1976, p. 185) defined the equation $ed = em + ee$ to describe this, where ed stands for "energy that is directly productive" (p. 185), em

stands for energy required to maintain the existing resources of the organism, and *ee* stands for "expansive energy, the energy available for growth and reproduction" (p. 185, emphasis original). Hence, evolution is construable as the trapping of energy in the environment by organisms — the success of which earns energy towards the maintenance and development of the individual and species — and competes against the energy-procuring potential of competing species.

The energy trapped in a living organism will not be released back into the environment until it dies, after which other organisms make use of it. Organisms can, of course, be killed by predators or parasites, essentially having their energy stolen. This brings us to the issue of trophic levels, and an opportunity to examine the trophic structure of the food web, a different kind of hierarchy [Hairston and Hairston, 1993]. Every ecosystem can be partitioned into a number of different "trophic levels" which define how energy flows within that ecosystem. These levels are determined by the way that the organism acquires energy [Hairston and Hairston, 1993]: usually with descending levels comprising carnivores, herbivores, detritivores, decomposers, and producers (who obtain energy directly from the sun). The exact number of levels will vary according to the ecosystem in question — forests are different from lakes which are different from jungles, oceans, deserts, tundra, etc. — and also the number of levels can vary because the ecologist can slice the levels into a number of different ways to capture different aspects of the many and complex connections of the food web. As a rule, energy tends to flow up the hierarchy (e.g. carnivores obtaining energy through predation), but as shown by Hairston and Hairston [1993], the hierarchy is not ladder-like, because there are multiple pathways for energy transfer (see figs. 1-3 therein), and these transfer are not only upwards, but downwards too (e.g. when carnivores die, they become part of the dead organic matter in the ecosystem, consumable by non-carnivores).

Moreover, energy transfer is not always associated with death or predation. For example, the transfer of energy may also be of some fitness *benefit* to the originator of the transaction (e.g. a mother bird feeding chicks or a fruit tree feeding birds), in which case we can think of it as analogous to a payment or a trade; that is, energy transfer can be understand from an economic perspective.

Taking this economics perspective, we can draw a strong analogy between the notion of fitness with the notion of *utility*, which economic agents attempt to maximize. Since utility embodies preferences for states of the world which can often be purchased using cash, economic actors can often increase their utility by increasing their wealth. 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. Like wealth, energy can 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. In a human 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 behaviors such as foraging, which mitigate against the risk of extreme events that would cause starvation or extinction [Bateson, 2002, Bednekoff, 1996, Brito e Abreu and Kacelnik, 1999, Harder and Real, 1987].

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 an organism can invest in a portfolio of foraging strategies in order to reduce variance in yield and hence reduce the risk of starvation; Real [1980] demonstrates a concave relationship between nectar yield and energy intake rates on bumble bees implying that optimal foraging for this species involves risk-averse optimization, and there is also strong evidence that our own species' omnivorous diet resulted from a need to hedge against the high-risk yield from hunting big game — the so-called "broad spectrum revolution" [Weiss et al., 2004].

Interestingly, risk-sensitivity can emerge even in the absence of non-linear utility or fitness functions. Niv et al. [2002] use a simulation model of bee foraging behavior in which bees are equipped with a simple reinforcement-learning algorithm in which the propensity to visit particular plants is updated dynamically as a function of a moving-window of yields. They show that this very simple learning algorithm gives rise to risk-aversion without any explicit risk-preferences or concave utility function. Chastain et al. [2014] show that population genetics models which incorporate sex are mathematically isomorphic with a very general machine-learning algorithm — *the multiplicative weights update* algorithm — which again gives rise to risk-sensitivity as an emergent property.

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 medium of exchange which explains social interactions in baboon societies. Nevertheless it is instructive to discuss the role of energy as a numéraire, firstly because it serves as a *store-of-value* in addition to a medium-of-exchange (that is, energy can be accumulated over time, and its inherent value in terms of fitness can be retrieved later on), and secondly because of its universal role across different species. The latter property allows for the possibility of an analog of trade throughout an entire ecosystem, and the possibility that this can result in a corresponding increase in the benefits resulting from mutualisms. We return to this discussion in Section 5.

4. Light-weight institutions

The concept of the so-called "free-market" is almost always an idealization. In practice, many modern markets rely heavily on contractual regulation and enforcement to, for example, prevent one party involved in a transaction from reneging on the other. Artificial markets are typically 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?

Ostrom [1990] argues that in human societies there are many approaches to resolving conflict when negotiating access to common-pool resources which do not require external governance over property rights, and that in contrast to full privatization of public goods, lightweight institutions evolve over time through a process of self-organization. For example, Berkes [1986] describes how a tragedy-of-the-commons was averted at an inshore fishery in Alanya (Turkey) in which the right to fish at a particular spot is initially allocated by a lottery held at the beginning of each season. Each day the fishers move to the next spot counter to the current direction of the fishes' migration. These conventions provide efficient utilization of resources, with

minimal conflict. A salient outcome from these arrangements is that for the most part the conventions are policed by the fishers themselves; cheaters who attempt to fish at the good spots are likely to be observed by the incumbent, and since the system is perceived as giving fair access to the most productive fishing sites, the rights of the incumbent to defend their spot is supported by the rest of the community. This in turn provides a sufficient disincentive to prevent attempts to cheat. Despite the lack of formal property-rights or centralized management this distributed self-organized institution was able to reduce conflict and increase the efficient use of resources.

Similarly, although we might not expect natural selection to produce fully-fledged markets which are fully regulated to ensure compliance with institutional rules, perhaps nature can produce analogs of some of the lightweight alternatives documented by Ostrom.

One possibility is that "trade" in nature could occur 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] and Hammerstein [2003a] note 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 narcotics ("black markets") in which the participants have no legal recourse in the event of a counter-party reneging. 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." [Hammerstein, 2001, p. 16]

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].

In many cases this kind of incremental reciprocity is integral to trading. For example, in many hunter-gatherer societies trade and reciprocity are mutually reinforcing, and it can be hard to draw a clear distinction between the two. Lee [1979] observed that the !Kung San often trade arrows in exchange for arrows, as summarized by Diamond [2013]:

> "It's even clearer that !Kung engage in extensive trade of arrows out of choice, because all !Kung make similar arrows, which they nevertheless trade back and forth between each other. Anthropologist Richard Lee asked four !Kung men to tell him who owned each of the 13 to 19 arrows in each of their quivers. Of the four men, only one (Kopela Maswe) had no arrows from other men. One man (/N!au) had 11 arrows from a total of four other men, and only two arrows of his own.

> The other two men (/Gaske and N!eishi) had no arrows of their own: instead, each was carrying the arrows of six other men. What is the point of these conventional monopolies and of arrow-for-arrow trading, seemingly senseless to us Westerners accustomed to trading only for objects that we can't readily provide for ourselves? Evidently, traditional trade has social and political as well as economic functions: not merely to obtain items for their own sake, but also to "create" trade for advancing social and political goals. Perhaps the foremost such goal is to *strengthen an alliance or bond* on which one can call if the need arises." [Diamond, 2013, Ch. 1, our emphasis]

Moreover, once trust has been established through reciprocity, fully-fledged trading of different commodities can flourish even in the absence of outside contractual-enforcement. In turn, further trading can enhance trust, and hence cooperation in other tasks.

Similar incremental approaches to trade occur ecologically. Friedman and Hammerstein [1991] analyze 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 fertilize 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].

Moreover, although contractual-enforcement cannot be imposed by outside agents, an alternative solution to the problem of contracts 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".

5. Efficient ecosystems

Mutualisms and reciprocal behavior are well-understood at the level of interactions between individual species or individual animals, but the implications of this work for the behavior at the level of *ecosystems* has only recently been modeled quantitatively [Zhang, 2003, Nathaniel Holland and Deangelis, 2009].

As previously discussed, there are two aspects of cooperative behavior: on the one hand, the elimination of cheats who exploit the benefits produced by the group, and on the other, how those benefits first accrue [Calcott, 2008]. In economics, the latter benefit is called the *social surplus* and microeconomic theory shows that, under some strong assumptions, competitive markets, which are populated by selfish economic actors, can maximize the social surplus in a competitive equilibrium; that is, we say that the market is *efficient*. These results are often put forward to argue (controversially) for a "free-market" approach to resource allocation, on the grounds that selfish behavior at the level of individuals results in the best possible outcome for society as a whole, despite the lack of an exogenous agent which selects for efficient outcomes.

By an analogy with microeconomics in which firms correspond to animals, and the market corresponds to an ecosystem, we can ask whether *ecosystems* are efficient. That is, we can attempt to understand the

conditions under which the benefits of a combination of mutualistic interactions are maximized, despite the absence of direct selection pressure for such. Rather than examining the energy or fitness accruing to individuals, we seek to understand how these benefits are distributed across the entire ecosystem, and the conditions under which this aggregate "social surplus" can be maintained. For example, we can ask whether there are particular combinations of mutualistic and competitive interactions between different species that maximizes the total number of individuals, or the total biomass, of the ecology as a whole.

The traditional model for understanding the dynamics of ecosystems is the Lokta-Volterra model. In a typical Lokta-Volterra model the trophic interactions between species are modeled as constant coefficients which specify the rate at which one species can grow by e.g. feeding on another. This typically leads to oscillations in the population levels over time, which are often well below the carrying-capacity for each species.

Zhang [2003] argues that this is too simplistic, since inter-specific interactions often consist of a subtle combination of competitive and mutualistic behavior, for precisely the reasons we have already discussed; for example, although rodents eat seeds, they also disperse them, and although herbivores eat grass, they also promote its growth. Moreover, the extent to whether competition or mutualism dominates between species will vary depending on population densities which are constantly changing. In the case of grazing for example, over-abundance of herbivores leads to a decline in grass density, but a complete absence of herbivores is equally harmful; the grass species does best for intermediate levels of grazing. Accordingly Zhang [2003] modifies the Lokta-Volterra model to allow for parabolic response functions and for the signs of the responses to change over time as an inter-specific interaction changes between predominantly mutualistic verses predominantly competitive. The salient result from this analysis is that this leads to an increase in the *overall* population of the ecosystem and stable co-existence of competing species, as compared with the traditional Lokta-Volterra analysis. That is, a combination of mutualistic and competitive interaction results in a greater "social" benefit as well as greater biodiversity and hence complexity, *without being directly selected-for by evolution.*

6. Honest-signaling and efficiency

One of the key concepts in microeconomics 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 incentivize *honest signaling.* 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 one 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.* In its original formulation, a mechanism design problem implies the existence of a designer who can choose rules which maximize allocative efficiency. However, it may be more appropriate to view real-life market mechanisms as self-organized institutions in

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

which market mechanism arises from co-evolution between signalers and allocators [Phelps et al., 2002, Cliff, 2003, van den Bergh and Stagl, 2003, Marks, 2006, Phelps et al., 2010].

We observe similar signaling 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 Zavahi [1997][4] conjecture that this signal bears a corresponding cost (the danger of the cry attracting predators), and that truthful signaling is an ESS of a strategic signaling 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 associate cost, or *handicap*, then truthful signaling can co-evolve between self-interested parties. Similarly we can think of the payments attached to bids in a conventional auction as "handicaps" which incentivize honest signaling in human marketplaces [Phelps, 2008, p. 25].

Artificial markets typically become more efficient as the number of participants increases. This is because the resulting competition reduces the market-power of any single individual; that is, the ability to manipulate prices in their favor through monopoly or oligopoly effects. Market power can be reduced, and both allocative efficiency and liquidity increased, by aggregating buyers and sellers in either space or time.

In nature, aggregation of signaling behavior is typified by species who adopt a mating system called a lek. In a lek mating system many males congregate together on the same site in order to court females through signaling displays. Females may visit several males on any given lek, but typically they will only copulate with one of them. Moreover, most matings are performed by the same male. There are many possible explanations for this behavior, none of which have been proven, but an intriguing possibility is that "females have a preference for male aggregations because these facilitate mate choice" [Davies et al., 2012, p. 271]. Patricelli et al. [2011] take this explanation to its logical conclusion by putting forward the hypothesis that lek mating systems are, in effect, auction marketplaces in which males signal competitively with each other; the highest bidder, i.e. the male with most ostentatious display and hence the largest handicap, "wins" the auction for mating-rights with the female. There is some empirical evidence supporting this hypothesis; female mate-choice in fiddler crabs is affected not only by features of any given male, but also its spatial neighbours [Callander et al., 2013]. An interesting research question is whether the distribution of male copulations in a lekking species could be explained using an auction-theoretic model in which the solution-concept is ESS, in place of Nash equilibrium used in neoclassical economics.

Collectively, we can think of the above factors as constituting the "market structure" of ecological interactions. In human societies, appropriate market structure can promote growth and diversity of the economy. As discussed, market mechanisms that promote efficiency do not necessary need to be designed, since they can arise between co-evolution between self-interested parties [Phelps et al., 2010]. This view of evolutionary mechanism design promoting efficient ecosystems can be nicely summarized using the analogy of Maynard Smith and Szathmáry [1995] in which they ask the question as to whether the rules governing human societies resemble a house or a termite mound:

> "A termite mound differs from a house in that no individual has an image of the final structure, which, although highly functional, emerges from the interactions of millions of individuals, whose behavior is law-governed but no influenced by any such image. In contrast, an architect starts with an image of the final building, which is functional because of his rational thought, and not through

[4] p. 120

the naturally-selected but blind behavior of the builders. Does society resemble a house or a termite mound?" [Maynard Smith and Szathmáry, 1995, p. 273]

Whilst there is no empirical evidence which can definitively answer this question, we have seen that there are plausible models of how market mechanism can potentially evolve in a self-organized fashion in both human, and non-human interactions.

7. Conclusion

Both biological and economic systems exhibit considerable diversity and complexity. Within the field of economics, it is increasing acknowledged that ideas from biology, such as natural-selection, are necessary in order to explain many of the complex-adaptive phenomena that are exhibited in markets [Beinhocker, 2007]. Conversely, we have argued that many ideas from economics, in particular comparative advantage and the resulting division of labor, are necessary in order to explain the complexity of ecological behavior and the biodiversity of ecosystems.

Indeed, from a complexity-perspective, we argue that it may be not be helpful to maintain a sharp distinction between the disciplines of economics and biology. As one of the anonymous referees remarked, *"Markets can arise spontaneously whenever individuals are able to engage in voluntary exchange and when they differ in their preferences and holdings. When the individuals are people, it's economics. When they're not it's biology"*. In this paper, we have reviewed some of the commonalities and differences between these two domains. Although the sophistication of market organization in non-human species clearly does not rival our own, there is nevertheless much to learn from applying economic thinking to nature. In particular, ideas from economics can help to address the "second problem" of cooperation [Calcott, 2008], viz. how the benefits of cooperation first arise. For example, by viewing ecological interactions in terms of market-efficiency we can examine how benefits accrue across the ecosystem as a whole. When larger social surpluses are generated, this can, in turn, mitigate the social dilemmas between individuals, resulting in greater cooperation and complexity.

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