Biological Markets, Cooperation, and the Evolution of Morality

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ABSTRACT

Biological market theory has in recent years become an important part of the social evolutionist's toolkit. This article discusses the explanatory potential and pitfalls of biological market theory in the context of big picture accounts of the evolution of human cooperation and morality. I begin by assessing an influential account that presents biological market dynamics as a key driver of the evolution of fairness norms in humans. I argue that this account is problematic for theoretical, empirical, and conceptual reasons. After mapping the evidential and explanatory limits of biological market theory, I suggest that it can nevertheless fill a lacuna in an alternative account of hominin evolution. Trade on a biological marketplace can help explain why norm-based cooperation did not break down when our Late Pleistocene ancestors entered new, challenging social and economic environments.

1 Introduction

Biological market theory (BMT) aims to explain the evolution and stability of cooperation by reference to ecological equivalents of economic market effects. After a slow start in the 1990s, BMT has in recent years become an influential

framework for the study of social evolution, having drawn support from further theoretical and empirical studies. BMT's rather quiet ascent compared to the tumultuous debates over group- and kin-selection theory might help explain why it has received little to no attention in philosophical discussions of social evolution (Okasha [2006]; Birch [2017]).[1] This paper aims to show that BMT merits close philosophical scrutiny, particularly in relation to 'big picture' accounts of the evolution of hominin cooperation and morality.

The present article focuses on one such comprehensive account, developed by Nicolas Baumard, Dan Sperber, and Jean-Baptiste André (among several others). They make heavy use of BMT in an attempt to explain the origins of fairness concerns in the course of hominin evolution. I will argue that this account runs into severe problems related to its application of BMT as well as regarding the explanatory power that is attributed to it. On the one hand, this will give reason for scepticism about the plausibility of Baumard *et al.*'s overarching claim that biological market effects have been a key driver of hominin social evolution. On the other hand, these pitfalls point to the explanatory potential of BMT in other, more restricted contexts. More specifically, I will suggest that BMT can fill a lacuna in another big picture account of hominin evolution. Building on recent work by Michael Tomasello and Kim Sterelny, I will outline a scenario in which biological market effects help explain the stabilization of norm-based cooperation at a particular stage in hominin evolution.

Before we take a closer look at the principles of biological markets, it will be helpful to sketch the contours of the account of Baumard and his colleagues, the analysis of which will comprise the bulk of the paper. Their account is complex and multifaceted: it draws on insights from mathematical modelling, anthropology, behavioural ecology, economics, and cognitive science. From this combination of inputs, Baumard *et al.* construct a scenario of the evolution a shared, intuitive sense of fairness under selective pressures for participating in cooperative endeavours with mutual fitness benefits.[2] These interactions, they argue, were market-based: supply-and-demand effects determined how the spoils from cooperation were divided. The hominin lineage started out from a baseline of market-based interactions that we still see reflected in our closest primate cousins. These simple biological markets fuelled cognitive investments in reputational concern. When market-based trade began to expand in size, scope, and diversity in the course of hominin evolution, this put an increasing strain on a purely strategic, reputation-based

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[1] Fraser's ([2013]) discussion of false advertising in biological markets is an exception, but even he is not concerned with biological market theory as such. His focus is on partner choice: a necessary but insufficient condition for a biological market, as we will see in Section 2.

[2] Because of the mutualistic nature of the interactions, the authors sometimes refer to the theory as a 'mutualist approach to morality' (for example, Baumard *et al.* [2013]).

management of cooperation. At this point biological markets began to select for a genuine sense of fairness about dividing the spoils from cooperation.

Baumard *et al.* have presented and defended the different components of their overall picture in over a dozen articles. Each of these caters to a particular (disciplinary) audience while drawing connections to the broader aims of the project. For purposes of discussion in this article, we can distinguish between three theses that Baumard *et al.* develop:

> The Market-Model Thesis: Formal evolutionary models show how biological market dynamics can favour the evolution of (preferences for) equitable divisions. Given a context of variable supply and demand among individuals from two trading classes, with individuals from at least one class being able to choose which individuals from the other class to partner with for a cooperative endeavour, the division of the spoils from cooperation will evolve to be proportional to each individual's investments. The division at evolutionary equilibrium corresponds to our intuitions about fairness (André and Baumard [2011a], [2011b]; Debove, André and Baumard [2015]; Debove, Baumard and André [2015], [2016], [2017]).

> The Evolutionary Continuity Thesis: The common ancestor of humans and great apes (and possibly an earlier ancestor shared with other simians) already participated in biological market-based exchange. In the course of hominin evolution, market-based interactions became an increasingly central feature of hominin lifeways. The scale, scope, and diversity of market-based interactions expanded (Baumard [2010a], [2010b], [2016]; Baumard *et al.* [2013]).

> The Reputation-Escalation Thesis: The gradual elaboration of market-based interactions instigated an arms race of capacities for reputation monitoring and reputation building in hominins, to the point where investing in reputational concern became prohibitively expensive. Instrumental preferences for looking fair only when being watched by others gave way to non-instrumental preferences for being fair. Hence, the human sense of fairness evolved under selective pressure from the demands of increasingly competitive biological markets (Baumard *et al.* [2010]; Baumard and Sperber [2012]; Sperber and Baumard [2012]; Baumard *et al.* [2013]; Sheskin and Baumard [2015]).

Together, these three theses appear to form a tightly interconnected account of the market-driven evolution of human fairness. The market-model thesis provides a theoretical basis for the genealogical narrative about hominin evolution that is presented as the evolutionary continuity thesis, which in turn

supports the moral-cognitive transition that is argued for through the reputation-escalation thesis.

However, on closer inspection the three theses turn out to suffer from serious problems, both individually and in combination with each other. The pivotal issues derive from Baumard *et al.*'s interpretation and application of BMT. I start by showing that the models they construct do not meet the basic conditions for being models of biological markets and therefore fail to provide the right kind of theoretical foundation for the other theses to build on. Next, I show that the evolutionary continuity thesis runs into its own, empirical issues: the extraordinary cognitive demands it places on our ancestors are demands they could not have met. This in turn removes essential support from the reputation-escalation thesis, which faces additional conceptual problems of its own. On one interpretation, the reputation-escalation thesis provides an explanation for the emergence of a hard-wired 'market sense' rather than an intuitive fairness sense; on the only other possible reading, it explains how a pre-existing sense of fairness became directly action-guiding and stopped being overruled by strategic concerns. Hence, on neither reading does the reputation-escalation thesis account for the origins of a genuine fairness sense.

In sum, I will argue that the account of Baumard and colleagues encounters a combination of theoretical, empirical, and conceptual hurdles that render their overall account of the market-driven evolution of an intuitive fairness sense deeply problematic. I will provide a detailed assessment of the three theses and their problems in Sections 3 to 5. Having thus mapped a range of restrictions and provisos for the successful deployment of BMT, I show in Section 6 how it can nevertheless help advance our theorizing about hominin moral evolution in a more restricted and targeted way. However, before entering this discussion of the (mis)uses of BMT we need an understanding of its elements. So let us first consider the basic conditions for biological markets.

1.1 Conditions for biological markets

The very idea of a biological market challenges an assumption in economics that traces back to Smith ([1776], I.I.2), who famously stated that 'the propensity to truck, barter, and exchange one thing for another [...] is common to all men, and to be found in no other race of animals'. In the early 1990s, Noë and Hammerstein (Noë *et al.* [1991]; Noë and Hammerstein [1994], [1995]) challenged this assumption by suggesting that the basic requirements for market-based exchange could in certain conditions be met by non-human animals.

The development of BMT by Noë and Hammerstein was prompted by the problem of defection in dyads of non-kin. Trivers ([1971]) famously proposed that cooperative interactions between pairs of individuals could evolve through reciprocity: if the expected fitness cost of a helping behaviour is

lower than the expected fitness advantage to the recipient, the helping behaviour will evolve when it is reliably reciprocated.[3] In other words, reciprocity requires an (evolutionary) expectation of mutual benefit. But reciprocity doesn't come for free: benefitting from one's partner's help without returning the effort is even more advantageous. Trivers's proposal therefore fueled many well-known modelling efforts and theoretical extensions to account for the evolutionary stability of reciprocity (Axelrod and Hamilton [1981]; Alexander [1987]; Nowak and Sigmund [1992]; Dugatin [1997]). Virtually all of these followed the example Trivers's had set in considering strategies of cooperation and defection for individuals in fixed and enduring interactions. Noë and Hammerstein argued that this focus on obligate partnerships explained why real-world examples of reciprocity remained few and far between: in reality, many organisms have considerable influence over which others to partner with and when to abandon a partner (Noë and Hammerstein [1994]; Noë [2006]; Carter [2014]). They thus argued for the relevance of partner choice and partner switching (in addition to partner control) in the study of cooperation. BMT developed from considering the dynamics of cooperation under this broader interpretation of reciprocity.

Consider the formation of mutually beneficial partnerships between agents of different trading classes, with members of one class having the opportunity to choose which members of the other class they opt to trade a resource or service with. Since the choosing individuals will profit from picking the best available partners, their potential partners will profit from competing to be chosen as a trading partner. Discriminative partner choice by one class thus triggers an outbidding competition in the other class. Those who can offer the desired commodities at the lowest 'price' will tend to be selected as partners and obtain benefits from trading. For this dynamic of partner choice and outbidding competition to result in market-based exchange, a further condition needs to be met. It must be possible for the supply/demand ratio of the traded commodities to change. This last condition permits the operation of a biological equivalent of the law of supply and demand. For example, if supply increases due to an increase in the number of potential trading partners, this will lower the price they can ask from the choosing agents (the demand side).

In sum, four basic conditions that must be met for a biological market to materialize (Barrett and Henzi [2006]; Werner *et al.* [2014]; Hammerstein and Noë [2016]; Noë and Kiers [2018]):

> Exchange and Trade: Individuals can be sorted into classes with
> different degrees of access and control over certain commodities

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[3] Trivers introduced the term 'reciprocal altruism' for interactions of this kind, but this terminology is considered misleading since no one is paying a net fitness cost (West *et al.* [2007]; Carter [2014]; Schino and Aureli [2010b]).

(resources or services). Individuals from one trading class can exchange commodities with individuals from at least one other trading class.

Discriminative Partner Choice: Individuals can compare offers and choose (or switch) between available trading partners in search of a better offer.

Outbidding Competition: There are differences in the profits individuals can reap from trading at a given rate of exchange of commodities (the 'price').

Supply/Demand Variation: It is possible for the supply/demand ratio to change and affect the price. For example, if it becomes cheaper to supply a certain commodity and demand is stable, the price will tend to drop.

When these four conditions are in place, an ecological equivalent of the supply and demand will determine the exchange value of the traded commodities, akin to bartering and face-to-face trading in human economic markets (Noë and Hammerstein [1995]; Noë [unpublished]). All else being equal, the forces of supply and demand push the price toward the point at which the level of supply and demand balance. The biological market is said to 'clear' at this market equilibrium, as in classical economic market theory.

There are important differences between the markets of biology and classical economics. Three key departures from classical economic markets are worth highlighting: biological markets do not require rational and cognitively advanced utility-maximizing agents, but can work with cognitively simple fitness-maximizing individuals; they do not incorporate explicit price mechanisms, but price setting is approximated by individuals' consideration of the state of the local market in their decision to accept or decline an (implicit) offer; and finally, since biological markets are not regulated by binding and enforceable contracts they are more vulnerable to cheating, exploitation, and extortion (Bowles and Hammerstein [2003]). This last point was Smith's prime reason for rejecting the idea of non-human markets out of hand. Modern economic theory, on the other hand, recognizes that contracts are often incomplete and their maintenance costly, and considers that agents tend to have limited information about other transactions in the market. Developments of this sort in the sphere of economics suggest that the conceptual and theoretical divide between economic and biological markets is less wide and deep than it may initially appear to be (Hammerstein and Hagen, [2005]; Hammerstein and Noë [2016]; Noë [unpublished]).

Over the last two decades, numerous observational studies and field experiments have been carried out to identify market effects in nature. I close this section with a few examples of biological markets that will prove instructive for purposes of contrast and comparison in later sections.

Most studies of biological markets have looked at interactions among non-human primates. A well-known case of a primate biological market comes from a field experiment with vervet monkeys. Fruteau *et al.* ([2009]) showed that a shift in food supply led to changes in the ratio of grooming that was exchanged for food, in line with predictions from BMT. Their experiment had two phases. In the first phase, they designated a single low-ranking female as food provider by training her to trigger the release of a large amount of food from a container. This 'provider effect' significantly increased the ratio of grooming given relative to grooming received for this female; her novel food-providing monopoly had given her strong leverage over grooming partners. In the second phase, the experimenters introduced another, equally rich food container of a different design. Another low-ranking female had been trained to open this box. Fruteau *et al.* found that this shift from a monopoly to a duopoly of food suppliers caused a drop in the grooming ratio for the first provider and increased the grooming ratio for the second provider, exactly as BMT predicts. Increased supply with stable demand resulted in a lower average food price.

It seems intuitive to look for market effects in primate species, on the expectation that satisfying the conditions for biological markets is limited to cerebrally advanced and behaviourally flexible species. However, one of the most prominent examples of a biological market comes from fishes rather than primates. The poster child of BMT is the interspecific mutualism between the cleaner wrasse *Labroides dimidiatus* and 'client' reef fish species. Cleaners are territorial and usually occupy fixed territories of a few cubic meters on a coral reef. Clients queue at these 'cleaning stations' to get their skin cleansed of ectoparasites, which form a major component of the cleaners' diet. Client fish come in two variants: 'choosy' species whose territorial range includes several cleaning stations and 'resident' species that only have access to one cleaning site. These circumstances set the stage for an outbidding competition with market effects (Bshary [2001]). Queueing clients compete over access to a given cleaner, whereas the cleaners compete against each other for access to the choosy clients. A cleaner that fails to discriminate between choosy and resident clients risks losing the choosy individuals to a competing cleaner at a nearby cleaning station. Cleaners therefore tend to respond to the presence of choosy species by cleaning them first and by providing a higher quality cleaning service than they give to resident clients (Bshary and Grutter [2002]). This behaviour cannot be accounted for by differences in the food patches that individuals constitute: even when residents carry more ectoparasites than choosy individuals they fail to gain priority in the cleaning queue. This suggests that the cleaners are treating choosy clients as social partners with outside options. Cleaners respond to a changing market place: an increase in competition with other cleaners through the appearance of choosy clients (that is, an increase in supply of cleaning

opportunities) induces them to lower the average price of the cleaning service (Bshary and Schäffer [2002]; Adam [2010]).

The cleaner–client fish mutualism evinces that cognitive sophistication isn't of overriding importance to get a biological market going. Whether or not market effects can arise will also depend on the nature of the traded commodities and the structure of the trading environment, to mention just two factors. The cleaner–client fish market is facilitated by the instantaneous and simultaneous distribution of the traded commodities: the cleaning service constitutes the provision of food.[4] This obligate simultaneity of the transaction eliminates the possibility for cheating that exists in delayed, contingent exchange. The structure of the trading environment also helps. It is relatively easy for cleaners to monitor the state of the local market, since cleaning only happens at fixed cleaning stations; a growing queue of clients waiting to be cleaned is an unambiguous sign of increasing demand. Finally, cleaners can often rely on easily discernible and robust differences in morphology between choosy and resident clients to reliably tell their different kinds of customers apart (Bshary and Schäffer [2002]; Bshary and Noë [2003]).

In Section 4, I will return to this observation that the satisfaction of the conditions for market-based exchange isn't only—or even primarily—a cognitive affair. But first, let us consider the application of BMT by Baumard and colleagues in their modelling exercises, which they present as the backbone of their hypothesis about the role of biological markets in human evolution.

2 Modelling the Cooperation Market

2.1 Cooperation markets and the evolution of equitable divisions

Baumard and colleagues take up BMT to model what they call 'cooperation markets': scenarios in which individuals compete for participations in cooperative ventures, the surplus of which needs to be divided in some way. If a pair of individuals with equal bargaining power has to repeatedly bargain over how to divide a pool of resources that they have harvested cooperatively, they will evolve to agree on dividing the spoils equally (Rubinstein [1982]). In the long term, neither party can force the other into accepting less than half. But what if there exist strong asymmetries between interacting individuals? Baumard *et al.* aim to show that even if within pairs some individuals have more bargaining power than others, market effects can prohibit them from exercising their power. In biological cooperation markets individuals reliably evolve a disposition to share equitably.

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[4] At least this holds for the standard cases of ectoparasite removal. Cleaners can also take bites of mucus tissue, which is not a service to the client. For further discussion of opportunities for free-riding in contexts of partner choice, see (Fraser [2013]).

Consider the simplest market model they offer in support of this claim (André and Baumard [2011b]). The model is based on the dictator game: a proposer determines the division of a bundle or resources between itself and its partner (its responder), who is forced to accept the proposed division. In a standard (non-iterated, anonymous) dictator game the most successful proposers will be those that make maximally unfair offers, leaving the smallest possible amount of the resources to their responders. André and Baumard explore what offer levels evolve when these games are iterated and modified to allow for partner choice.

The basic setup is as follows. In each round of the game, responders can team up with proposers in exchange for a share of the cooperative benefits. Proposers first announce their genetically set offer levels. Next, responders are asked one-by-one and in random order to team up with a proposer until no further pairs can be formed. Responders are utility maximizers: they choose to partner with the most generous proposer available. At the end of each round, individuals reproduce asexually and in proportion to the amount of benefits they have obtained. Offspring inherit their parent's genetically encoded offer level with a small probability of mutation.

André and Baumard argue that this setup satisfies the essential conditions for a biological market. Proposers and responders form two trading classes, responders compete for access to the most generous proposers, and the density of proposers and responders can be interpreted as setting the level of supply and demand, respectively. We can also think of proposers' offer levels as determining the 'price' of an interaction. A proposer that is disposed to offer less than half of the benefits sets a high price: the return on investment from cooperating with this proposer will be low. A proposer that offers more than half sets a low price.

Using this basic setup, André and Baumard ([2011b]) first consider how prices evolve in a population where supply and demand are fixed exogenously. Consider a population whose level of supply is lower than its level of demand: responders outnumber proposers by a fixed proportion. In this population, all proposers will find a responder to interact with, but some responders will be left out in the cold, unable to reap benefits from teaming up with a proposer. Given such a situation of high demand for proposers, a stingy mutant proposer has an advantage. By making offers slightly below the average offer level of resident proposers, stingy mutants will obtain a slightly above-average share of the benefits. Over time, the invasion of mutants will cause offer levels to drop to the point where responders receive the smallest possible returns from pairing with a proposer. The opposite happens in a population where the level of supply is fixed to be higher than the level of demand: proposers outnumber responders. Since in this population proposers will have to compete for responders, mutant proposers that make slightly higher-than-

average offers will have an advantage. Selection for ever more generous mutants thus causes offer levels to skyrocket: proposers end up making offers as high as they can to attract responders. In sum, when levels of supply and demand are fixed exogenously at unequal levels, divisions will evolve to be maximally unfair. The price of interacting with a proposer will end up being either maximally high (when demand outstrips supply) or extremely low (when supply outstrips demand).

But what happens to prices if the level of supply and demand can change? That is, what if individuals can choose which trading class to play in, based on information about average expected payoffs from each class? André and Baumard show that in this case the offer level will affect the density of players in each class in such a way that the expected payoffs for individuals in each class will equalize within each generation. That is, for each genetically programmed offer level, the population will move toward a particular 'ecological equilibrium' of proposers and responders. Next, André and Baumard show how, in evolutionary time, selection on slight mutations will affect the offer levels proposers make. Selection moves the population along a series of ecological equilibria to the 'market equilibrium' at which proposers make offers of equal splits with responders.

Again, this outcome can be grasped intuitively. Consider a population in which proposers start out by offering less than half of the benefits from cooperation to their partners. This makes it profitable for individuals in the responder role to switch to the proposer side. The proportion of proposers increases, which causes the average payoff from playing in the proposer role to drop: some proposers won't be able to find a responder to team up with and thus get zero benefits from cooperation. It stops being advantageous to switch between trading classes when the average payoffs for proposers and responders balance. This is the ecological equilibrium for the offer level: the point at which the proportion of individuals in each trading class is such that no individual has an incentive to switch classes.

Each average offer level has its own ecological equilibrium. For offer levels of less than half (high prices), it follows that the lower the offer level, the more proposers will outnumber responders at ecological equilibrium: a higher payoff from partnering with a responder compensates for a higher risk of not finding one (Figure 1a). The opposite holds for average offer levels of more than half. The higher the offers proposers are disposed to make (the lower the price they ask), the more individuals will play in the responder role at ecological equilibrium. The higher the payoff responders receive from partnering with a proposer, the more it pays for them to risk not finding a proposer to partner with (Figure 1b).

Before considering how the establishment of ecological equilibria for any given starting price-level feeds into the evolutionary dimension of the model,
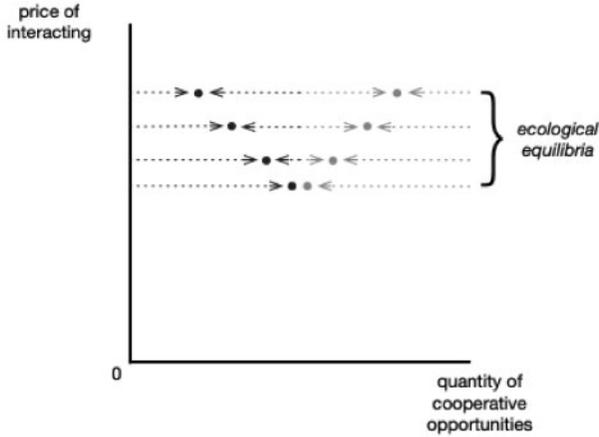
Figure 1a. Light dots represent the proportion of proposers, dark dots the proportion of responders. The figure shows four ecological equilibria for populational states in which proposers on average share less than half of the benefits with responders (high prices). The less proposers share—the higher the price they ask—the more they outnumber responders at ecological equilibrium.
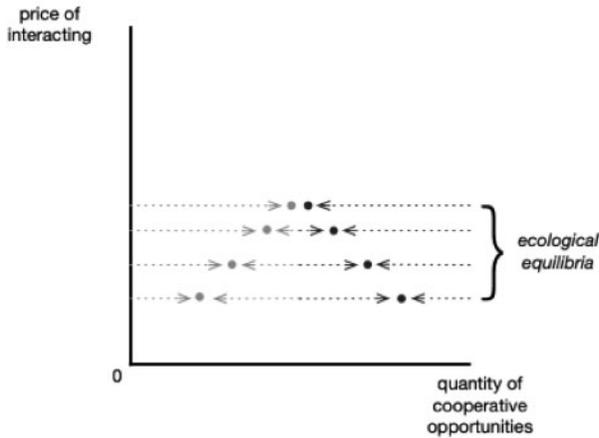

Figure 1b. Light dots represent the proportion of proposers, dark dots the proportion of responders. The figure shows four ecological equilibria for populational states in which proposers on average share more than half of the benefits with responders (low prices). The more proposers share—the lower the price they ask—the more they are outnumbered by responders at ecological equilibrium.

first notice that if we plot the ecological equilibria for different price-levels, a familiar pattern from classical economic market theory appears. The proportions of proposers at the equilibria for different prices line up along an upward sloping supply curve, the proportions of responders follow a downward
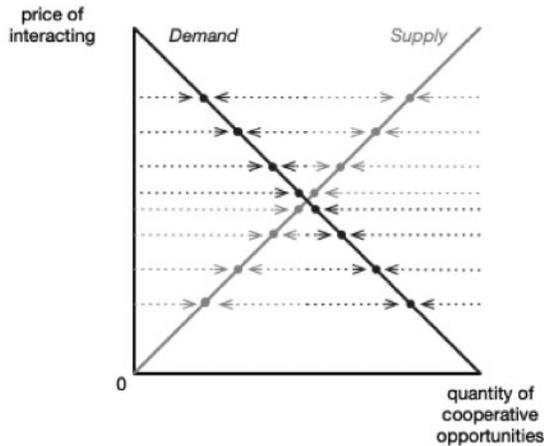
Figure 1c. Supply and demand 'curves' (straight lines in this case) connect the levels of supply (the proportion of proposers) and the levels of demand (the proportion of responders) for each price point.

sloping demand curve (Figure 1c). At the intersection of these 'curves'—straight lines in this case—lies the market equilibrium at which the division of the spoils from cooperation is equal. André and Baumard show that from any price-level that is taken as starting point, natural selection will push the population from its initial ecological equilibrium to the market equilibrium of fair prices.

Take a population in which the proposers start out making high offers (low prices) on average: this population balances at an ecological equilibrium of excess demand (Figure 2).

Since all proposers in this population are guaranteed to find a partner, stingy mutant individuals that are disposed to make slightly lower offers when playing in the proposer role will have a fitness advantage. However, as the average price of interacting with a proposer thus rises, the level of demand will drop, since individuals will increasingly opt to play in the proposer role. As a result, the population moves toward a new ecological equilibrium with a higher supply-level and lower demand-level. This selection for stingy mutants continues until the population reaches as state where mutants that ask still higher prices are no longer at an advantage because they be able to won't find a partner. This is the ecological equilibrium at which the proportion of proposers and responders is equal: the market equilibrium of equal division.

We see the opposite movement towards the market equilibrium in a population that starts out at an ecological equilibrium of excess supply (low prices). This population will be invaded by generous mutants that make slightly higher
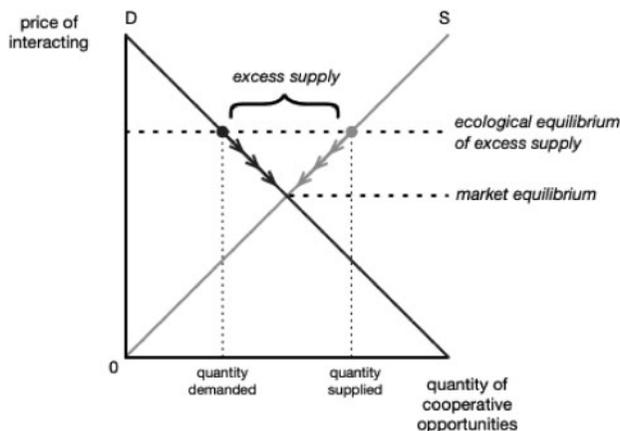
Figure 2. In a population that starts at an ecological equilibrium of excess supply, selection in favor of slightly lower offers will drive the population toward the market equilibrium of supply and demand.

offers when playing in the proposer role. André and Baumard show that their slightly lower gains from cooperation are offset by their increased chances of finding a partner compared to other proposers. As a result, this population will evolve along ecological equilibria of increasingly lower supply and higher demand, again until it reaches the market equilibrium at which the proportion of proposers and responders are equal (Figure 3). In sum: if demand outstrips supply, selection favouring stingy proposers moves the price up to the level of equal splits; if supply outstrips demand, selection favouring more generous proposers drives the price down to the level of equal splits. Hence, regardless of which ecological equilibrium the population starts out at, selection will drive the population toward the market equilibrium. André and Baumard ([2011b], p. 1451) thus conclude that their models have shown how 'fairness [can] evolve from any initial state, and is evolutionary stable'. Selection on random mutations to the offer level operates as 'an equivalent of the law of supply and demand' ([2011b], p. 1447).

2.2 Markets without market dynamics?

The model I have just described verbally relies on assumptions and idealizations that obviously limit its informativeness and scope of application. Baumard and colleagues are the first to admit this. For instance, they note that the idea of cost-free and unconstrained role-switching hardly applies to human interaction (André and Baumard [2011b], p. 1454). Over the years, they have elaborated the initial model in an effort to relax several such limiting
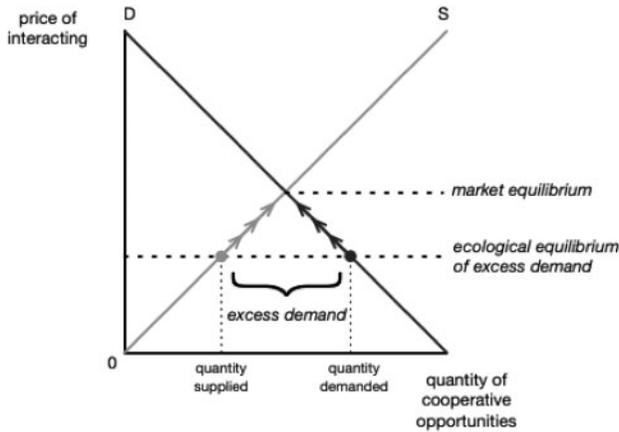
Figure 3. In a population that starts out at an ecological equilibrium of excess demand, selection in favor of slightly higher offers will drive the population toward the market equilibrium of supply and demand.

assumptions. For example, Debove *et al.* ([2015]) have shown that one need not make the 'highly debatable' assumption that all individuals have equal possibilities of choosing roles and partners. Even if there exist 'systematic asymmetries of strength' between individuals, equal divisions can evolve in a broad range of circumstances ([2015], p. 562). Another newer model shows that if individuals make unequal investments, selection favours proportional, equitable divisions rather than just equal ones (Debove *et al.* [2017]). These elaborations still leave us with many aspects of the models that could be questioned for their ecological validity (such as the assumption that choosing and/or switching partners is cheap: a key assumption that is needed to guarantee equitable outcomes). However, I want to raise a different issue. I want to consider not how instructive and robust the market models are, but whether they actually are what they are claimed to be: market models.

Baumard and colleagues are clear on this point: their models model markets in the sense of biological market theory. Not only do they state this explicitly, but we have also seen that the couch their explanations of the models in terms of 'prices', 'supply', 'demand', and 'market equilibrium'. This terminology notwithstanding, it is unclear how their models are supposed to demonstrate genuine market effects in the evolution of equitable outcomes. For a crucial feature is missing from the models that I have just described: an account of what happens when supply or demand as such shift, that is, when the ratio of supply and demand changes. On closer inspection, it becomes clear why this is missing: the models are constructed such that shifts in supply or demand cannot possibly occur.

To see this, let us return to the model from André and Baumard ([2011b]). We have seen that in this model a change in prices (through a genetic mutation) will affect the level of supply and demand. For instance, in a population with stingy proposers, which balances at an ecological equilibrium of an excess supply of cooperative opportunities, selection will favour mutations for generosity, which reduces the level of supply and moves the population toward a supply–demand balance. However, it is an elementary principle in economics that in order to meaningfully speak of 'supply' and 'demand', it must also be possible for these to change as such: the supply and demand curves must be able shift, and to do so independently (Frank *et al.* [2018]). We have seen examples of such supply and demand shifts in Section 2. When the supply of fish providing cleaning jobs or monkeys providing food increases, the average price of the commodity they offer drops. Yet, shifts of this kind cannot occur in the models of André and Baumard, since they define 'supply' and 'demand' in terms of each other, as the proportions of individuals in each role at ecological equilibrium. This entails that the only possible levels of supply and demand are those that fall on the lines that connect the ecological equilibria, as in Figure 1c. A shift in supply or demand would entail, absurdly, that certain market players have an undefined role *qua* market players (and the cumulative frequency of proposers and responders doesn't sum to unity) or that there are more market players than there are players (and the cumulative frequency of proposers and responders exceeds unity).

Since André and Baumard fail to define supply and demand coherently, it is misleading to speak of natural selection acting as a 'market force' that can move the price toward a 'market equilibrium price' of equal division. To meaningfully speak of market forces and equilibrium prices, it must be possible for market dynamics to be responsive to shifts in supply or demand, and for the equilibrium price to be affected by such shifts. In contrast, the fixity of 'supply' and 'demand' in the models of André and Baumard guarantees that there is only one equilibrium price: an offer of exactly half of the resources. Put differently, the evolution of preferences for equity is not due to market effects, but due to their absence!

This problem is even more conspicuous in the later models of Baumard and colleagues (André and Baumard [2011a]; Debove, André and Baumard [2015]; Debove, Baumard and André [2015], [2016], [2017]). In these newer models— variants of ultimatum games rather than dictator games—individuals are paired up randomly before within each dyad each individual is assigned to a role. The individuals playing as proposers make their (genetically encoded) offers. If the offer level is on or above the responders' acceptance threshold, the offer is accepted and implemented. If it falls below the threshold, the responder will decline the offer and both individuals incur a small cost to find a new partner. Individuals reproduce in accordance with the number of

successful social interactions they have had in their lifetime. Like the model from André and Baumard ([2011b]), these newer models show that if the cost of switching partners is kept low, there will be selection for an expected payoff of (close to) half the resources.[5] Baumard *et al.* also present these models as market models, since 'supply and demand represented by the trading classes will determine the value of the exchanged commodity' (Debove *et al.* [2015]).

However, these models still define supply and demand in terms of each other, as proportions of the total population. Moreover, by sorting all individuals into pairs before offers are made they stipulate even more conspicuously that supply and demand are always exactly balanced. Hence, puzzlingly, the 'market' has only a single price equilibrium. Again, this can only mean that we are not dealing with a market in the first place. Baumard *et al.*'s market models are not the genuine article.

At this point, one might be tempted to respond that Baumard *et al.* could just retract the 'market' label (or suggested they were using it in a loose and metaphorical sense) and argue that their models nevertheless show how a combination of partner choice and role choice can lead to equitable outcomes. Yet, when we situate the models in the context of the broader framework that Baumard *et al.* aim to develop, a response along these lines becomes rather problematic. First, it would mean that the models become irrelevant to the overall project they are pursuing. It would be to give up on the claim that the models support the overarching project of showing that equitable outcomes will evolve under genuine market dynamics, of the sort described by biological market theory. Second, it would arguably provide a weak foundation for an alternative big picture account of the evolution of fairness concerns. For, by making it a precondition that supply and demand are always exactly balanced, the models do not just incorporate a questionable empirical assumption, but also effectively assume perfect (global) equality of opportunity to explain equality of outcome in cooperative ventures.[6] This erodes the relevance of the models for any big picture account of hominin evolution, which surely requires explaining—rather than assuming—these aspects of cooperation.

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[5]   It is harder to give an intuitive rendering of why equal (or, in case of unequal investments: equitable) divisions evolve under these conditions. Fairly complex dynamics arise from the simultaneous evolution of offer and response parameters. The model of André and Baumard ([2011b]) was easier to grasp on an intuitive level, since it only involved the evolution of the offer parameter.

[6]   André and Baumard ([2011a], p. 132) are explicit about this: 'The emergence of fairness thus crucially relies on the fact that all individuals have a fair chance of playing both roles in each interaction'. Although in later models they show that fairness can also evolve if some individuals have a higher chance of being assigned to the proposer role, this result still depends on the assumption that the class of responders and proposers will be equally large. That assumption alone is sufficient to grant global equality of opportunity to cooperating individuals.

3 Markets and Evolutionary Continuity

In the previous section, I argued that since the market-model thesis is not supported by Baumard *et al.*'s models, this removes one pillar of support from their big picture account of the biological market-driven evolution of fairness. In this section, I will argue that the continuity thesis also runs into problems with regard to its use of BMT. But before doing so, I want to briefly consider the interface between these two theses. Baumard *et al.* tell us surprisingly little about how the market-model thesis as such (regardless of its evidential status) is supposed to provide a theoretical backdrop for the evolutionary continuity thesis. However, what they do say gives us reason to think that the connection between the theses is problematic.

The market-model thesis, they tells us, is aimed at modelling 'ultimate biological markets [where] the 'bargaining' already took place at the ultimate level by means of natural selection [...] the result of this bargaining is the existence of a genuine sense of fairness which 'automatically' makes humans prefer equitable strategies' (Debove *et al.* [2017], p. 11). Baumard *et al.* explicitly contrast these ultimate biological markets where selection favours automatic, inflexible dispositions with proximate biological markets where individuals flexibly adjust the price they pay to changes in supply and demand (as in the examples from Section 2). Yet, in drawing this contrast they overlook that it exposes a glaring disconnect between the two theses, since the evolutionary continuity thesis is clearly a thesis about the expansion of proximate biological markets. If the evolutionary continuity thesis is to be believed, it was exactly the increasing importance and centrality of bargaining between individuals within their lifetimes that set hominins on a different evolutionary track. This disconnect between the market-model and evolutionary continuity theses suggests that the account of Baumard *et al.* is much less tightly integrated than they make it seem. The results that the market-model thesis was supposed to provide cannot be the kind of results that support the evolutionary continuity thesis. This gives us further reasons to put market-model thesis aside and consider whether Baumard *et al.* can marshal sufficient evidence for the market-driven history of hominin evolution on the basis of the evolutionary continuity thesis alone.

Of the three theses I distinguished, the evolutionary continuity thesis has been developed the least by Baumard *et al.* Although their writings are full of scattered references to the purported gradual expansion of hominin biological markets—in terms of the diversity of traded commodities, the number of trading opportunities, and dependency of individuals on trade—they do not provide evidence for this in the form of a systematic genealogical account. We learn little more than that market-based trade in non-human primates is 'no doubt the closest thing to morality that has been observed in non-human

animals' (Baumard [2016], p. 196) and that there exists 'a genuine continuity between non-human animals and humans in this domain [. . .] animal cooperation and human cooperation may have followed the same evolutionary pathway, differing only at the proximal level (scale of cooperation, psychological mechanisms)' (Baumard [2010b], p. 5).

There are good reasons to be sceptical of even this thin account of evolutionary continuity. The evidence for the baseline is weak, as is the support for the hypothesis that there was gradual increase in complexity of biological markets. Baumard ([2010a], [2016]) cites several studies in support of their claim that there is solid evidence for a baseline of already quite sophisticated primate biological markets (PBMs) where individuals trade two or more commodities. They note that several studies have shown that monkeys and apes trade commodities such as grooming, sex, meat, agonistic support, and access to infants. However, apart from artificial field experiments like those of Fruteau *et al.* ([2009]) that we saw in Section 2, the evidence for genuine market effects remains scarce. Methodological concerns about measuring exchange (which I won't review here) have been a subject of ongoing discussion (Sánchez-Amaro and Amici [2015], [2016]; Dunayer and Berman [2016]; Kaburu and Newton-Fisher [2016]). But apart from methodological concerns, there are pressing theoretical and empirical reasons to doubt that monkeys or apes can engage in the market-based trade of even this limited range of commodity. In their excellent review of PBM studies, Sanchéz-Amaro and Amici ([2015], p. 54) note that if, say, grooming can be traded for two or more other commodities, it quickly becomes very difficult to establish how its value changes under fluctuations in supply and demand: 'If grooming can be traded for different commodities (e.g., grooming, food, tolerance at feeding or drinking sites, access to infants, preferential mating, agonistic support), which percentage of grooming given should we correlate with the amount of each commodity received, when testing BMT?'. The problem is aggravated by differences in the time-frames at which different pairs of commodities are traded, and by the trading of the other commodities against each other. For example, although isolated studies have described chimpanzees as trading agonistic support and food for grooming, food for sex, and sex for grooming, the combination of these results amounts to a very implausible picture of what chimps are capable of. It would be astounding if they could reliably track and respond to the complex, interacting changes in supply and demand that will be manifested in the overlapping exchanges. It would be a stretch to think that even humans could pull this off in the absence of elaborate forms of book-keeping, price mechanisms, and monetary currencies.[7]

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[7]   Some have argued that chimps and other primates rely on capacities of 'emotional book keeping' to estimate partner-value in a way that fuels outbidding competition and is responsive to changes in supply and demand (De Waal [2000]; Schino and Aureli [2009], [2010a]). But as

Perhaps certain non-human primates engage in market-based exchange in isolated and controlled contexts, as with the vervet monkeys from the study of Fruteau *et al.* ([2009]). But these markets don't scale. Just adding a single additional tradeable resource to a local dyadic market requires individuals to track and update three prices instead of one, while the increased spatio-temporal scale of transactions exacerbates the problem of tracking what has been paid by and to others. More generally speaking, market mechanisms quickly become strained when different resources are exchanged at different time scales, in different combinations, and in different, changing locations. These problems of scaling render the continuity thesis very implausible. In order for simple biological markets to have expanded in size, scope, and diversity to the extent that Baumard *et al.* imagine they did, robust pricing and policing mechanisms need to have been in place. Biological market dynamics on their own won't create these.

4 Markets, Reputation-Escalation, and Fairness

The issues with the evolutionary continuity thesis have direct implications for the plausibility of the reputation-escalation thesis. The nature of the interface between these two theses is clear and straightforward. On the overall picture that Baumard *et al.* argue for, the dynamic of expanding and intensifying hominin markets is what drives the escalation of reputational concern. The reputation-escalation thesis thus offers a (moral-)psychological complement to the socio-ecological backdrop of the evolutionary continuity thesis. If I am right that this backdrop is problematic, the reputation-escalation thesis comes under pressure too: it is no longer clear what drove the escalation of reputation such that it culminated in selection for a fairness sense.[8]

Let us set this problem aside for the moment and consider the reputation-escalation thesis in its own right. First, consider the thesis in more detail. As I mentioned in the introduction, the question Baumard and colleagues seek to answer with the reputation-escalation thesis is how hominins went from having a strategic preference for respecting other people's interests to having a genuine moral concern to respect those interests (Sperber and

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Sánchez-Amaro and Amici ([2015]) have pointed out, it is unclear how this mechanism is supposed to be responsive to changes in supply or demand. Does it respond to changes in the number of partners to competitors, or in the ratio? And how does it account for partners in the exchange of one commodity that are competitors for another?

[8] Notice the difference here with the interface between the market-model thesis and the evolutionary continuity thesis that I reviewed at the start of the previous section. We saw that those two theses mismatched on a conceptual/theoretical level. This is not the case with the connection between the evolutionary continuity thesis and the reputation-escalation thesis; the nature of the evidential relation between the two is clear. But precisely because of this, the problems with the former thesis do directly impact the plausibility of the latter.

Baumard [2012]; Baumard *et al.* [2013]). The answer, they suggest, centrally involves an arms race between capacities for reputation monitoring and reputation building. In the earliest hominin biological markets, individuals that monitored the behaviour of others in search for clues about their dispositions for generosity were at an advantage: 'In choosing a partner, one looks for relevant competencies and resources (which differ from one type of venture to another) and for cooperativeness or fairness, that is, for a reliable disposition to share the costs and to refrain from taking more than one's share of the benefits of cooperation' (Sperber and Baumard [2012], p. 507). The evolution of these 'evaluative functions of morality' in turn created selective pressures for individuals to behave so as to be chosen as partners in cooperative ventures.

Sperber and Baumard argue that, initially, reputation monitoring came down to tracking the past behaviour of others in search for clues about future cooperativeness. But as hominin markets became more expansive and complex, assessments of past performance became both less available and less reliable predictors of future cooperativeness: 'cooperativeness [could no longer] be effectively assessed without making inferences about others' mental states and dispositions' ([2012], p. 507). The evolution of mind-reading enabled hominins to better predict actions on the basis of inferred beliefs and desires. But mind-reading also turned hominins into better strategizers. Individuals became more adept at shaping others' beliefs about their own dispositions, to their own advantage. The result was a hominin world of Machiavellian strategizers who behaved like Hume's sensible knave: sharing fairly when their reputation was at stake but maximizing their own advantage otherwise. Yet strategizing has its limits: 'from a cognitive point of view, a Machiavellian strategy is a demanding one. It is often difficult to tell whether others are paying attention to our behaviour, and to predict how they might interpret it and what they would think or say about us as a result. Even if a Machiavellian agent cleverly manages to avoid being caught cheating, she might still behave in a way that suggests she is being clever rather than moral, and compromise her reputation as a result' (Sperber and Baumard [2012], p. 499). Thus, Sperber and Baumard argue, at some point the Machiavellian strategy became too demanding and too risky. When word about one's cheating behaviour could spread quickly, even a small glitch— behaving selfishly when someone happened to be watching—could turn one into a pariah and ruin one's chances of future cooperation. But when the Machiavellian strategy became ineffective, how else could individuals secure a reputation as a good cooperator?

> Is there a way cognitively easier and safer than a Machiavellian strategy
> to secure such a reputation? Yes: it consists in deserving it, that is, in

> having a genuine, non-instrumental preference for moral behaviour and a
> disposition to act on the basis of that preference. At the cost of missing a
> few opportunities for profitable cheating, a genuinely moral person is in a
> uniquely good position to be regarded as such. (Sperber and Baumard
> [2012], p. 499)

In short, when it became too costly to rely on an instrumental preference for
looking fair, it became advantageous to have a non-instrumental preference
for being fair. At some point in the hominin lineage, our ancestors evolved a
genuine fairness sense.

4.1 The target of reputational concern

Regardless of the empirical worries that could be raised about this transition
from strategizing to moralizing, I will argue that it founders on a conceptual
problem pertaining to the assumed target of reputational and moral concern.
We have just seen that Sperber and Baumard ([2012], p. 507) present the goal
of strategic reputation monitoring as that of determining whether others have
'a reliable disposition to share the costs and to refrain from taking more than
one's share of the benefits of cooperation'. But what is the capacity for recog-
nizing 'one's share' that features in this account of strategizing? The wording
suggests that even before a genuine fairness sense evolved, the division of
cooperative costs was already governed by some kind of shared (proto-)nor-
mative capacity. But given that this capacity cannot have been a full-blown
fairness sense, what kind of behavioural tendencies did it implement?

   To answer this question, we should zoom out to the big picture that
Baumard *et al.* argue for. Given their hypothesis that the evolution of repu-
tation management was driven by cooperation in a biological market, the
evolution of a capacity to contribute and receive 'one's share' must have
consisted in the capacity to monitor and respond to market equilibrium
prices. In other words, when Sperber and Baumard ([2012], p. 496) state
that Machiavellian strategizers aimed 'to merely *appear* to behave morally',
they must be speaking of individuals that asked and paid market prices when-
ever their reputation was at stake, but who tried to get away with paying less
(or keeping more) whenever they could.

   But now notice what this means for the transition from having an instru-
mental preference for looking fair to acquiring a genuinely moral disposition
for being fair. If taking and giving one's share is (implicitly) defined in terms of
asking and paying market prices, then the move from strategic behaviour to
moral behaviour must consist in a shift from only respecting market prices
when one's reputation is at stake to always following market prices, without
attempting to escape them strategically. In other words, if we follow the

reputation-escalation thesis to its logical conclusion, it points to the evolution of an always-on 'market sense' rather than a substantive fairness sense.

This conclusion is hard to square with our actual intuitions about fairness, which are not straightforwardly governed by dynamics of supply and demand (DeScioli [2013]; Birch and Witteveen [2017]). Moreover, it would be a stretch to think of departures from conformity to market prices as distortions or aberrations in the operation of our intuitive sense of fairness. Interestingly, Baumard ([2016]) himself has argued that a market sense does not equal a fairness sense, in his discussion of a classical study by Kahneman *et al.* ([1986]). Kahneman asked his participants whether it would be unfair for a hardware store to raise prices during a snowstorm. The majority thought this would indeed be grossly unfair. Baumard ([2016], p. 78) agrees, and presents this as an illustration of our unreflective, default intuitions about fairness: '[The store owner] is just taking advantage of a favourable balance of forces, and thus has no right to a larger piece of the common pie'. This seems at odds with his own theory. If fairness comes down to following the state of the market, we should consider the price increase fair. Alternatively, if acting like a true *Homo economicus* does not correspond to acting fair on an intuitive level (which it seems hard to doubt indeed!), the reputation-escalation thesis must be rejected.

There is no easy way out of this predicament for Baumard and his colleagues. Even if they were to drop the market-theoretic framework and propose another evolutionary driver of the escalation process, it is not clear how the reputation-escalation thesis could be redeemed as an account of the origins of fairness. The deep-seated problem remains that is a thesis about the disappearance of strategizing, rather than about the origins of intuitive fairness concerns. It is a thesis about how fairness intuitions stopped being overruled by strategic concerns and became directly motivating and action-guiding. It thus falls short as an explanation of the origins of fairness intuitions. Such an explanation would have to address how hominins went from being impulsive-driven 'wantons' (akin to other great apes) to becoming animals with moral cognition (cf. Kitcher [2006]).

5 An Alternative Scenario

The previous sections have shown that Baumard *et al.*'s account of the evolution of intuitive fairness concerns is deeply problematic. I have argued that the three theses that underpin their account run into severe problems, both individually and in combination with each other. My appraisal of the market-model and evolutionary continuity theses showed that the market-based backdrop of the account lacks theoretical and empirical support. My assessment of the reputation-escalation thesis revealed a further conceptual problem. This

thesis can at best explain the evolution of an always-on 'market sense'; it cannot account for the origins of an intuitive fairness sense.

Although this assessment presents a bleak prospect for a wholly biological market-driven account of the evolution of fairness, I will argue that the appreciation we have gained of the scope and limits of BMT does point to a more restricted role for BMT in theorizing about hominin evolution. In the remainder of this article, I will argue that BMT can help address a lacuna in an alternative kind of big picture account of the evolution of fairness. On this alternative account, biological markets are not presented as having driven the origin of fairness concerns, but rather as stabilizers of basic fairness concerns when these threatened to collapse in new and challenging hominin social environments.

5.1 Fairness before markets

An influential alternative picture of the evolution of fairness concerns has been offered by Tomasello ([2014], [2016]), who argues that collaboration rather than (market-based) exchange has been the key to the evolution of cooperation based on fairness norms. He suggests that changing ecological circumstances created tight interdependencies between early hominins, who became pressured to obtain a larger share of their food through active collaboration. At first, this perhaps took the form of group defence and scavenging hunts: loosely structured, cognitively undemanding performances in which it would have been beneficial to act together. These provided a platform on which more collaborative endeavours could be scaffolded. Perhaps around the time of *Homo heidelbergensis* some 400 kya, active hunting of large game had become an obligate component of the hominin social repertoire. Hunting demands close coordination. It drove selection for a capacity to put oneself into the shoes of one's partner, and to acquire a shared understanding of the roles that would be required for joint success. On a cognitive level, this translates into a capacity to form joints intentions with a partner. Individuals were thus enabled to recognize their partners as partners, rather than as social tools for individual success. Tomasello argues that it is only a small step from seeing someone as one's partner to seeing that partner as equivalent and equally deserving of a share the spoils.

Two aspects of this account are worth singling out. First, Tomasello argues that his account of cooperation is robust in evolutionary terms, since individuals cannot free-ride in cases of dyadic collaboration based on joint intentions. If either individual in a dyad fails to cooperate, the collaboration breaks down and there will be no benefits to divide. Success requires mutual effort. Second, Tomasello suggests that solving the problem of agreeing on what constitutes a fair division is easy. In early cases of collaborative foraging, with little to no

specialized tasks requiring special skills, each role counted for the same. The evolved sense of self-other equivalence would have impelled individuals to divide resources evenly.

Though I think that Tomasello's account of collaborative mutualism points in the right direction, he underestimates the problems of free-riding and division of the benefits. As Gintis ([2015]) and Sterelny ([unpublished]) have pointed out independently, Tomasello's solution to the free-rider problem lacks ecological validity. For collaborative scavenging and hunting of large game to have paid off, it must have relied on mobs rather than dyads. Only after the invention of specialized tools like spears and poisoned arrows could hunters perhaps have trimmed down group size to agile pairs with no room for free-riding. But these are Late Pleistocene circumstances, perhaps from after the projective revolution from around 70 kya (Sterelny [unpublished]). In the earlier Pleistocene environments that Tomasello is interested in, shirking or slacking was a live option. In groups of a dozen individuals on a hunt it would have paid off not to be in the front-line when approaching large game. The erosion of cooperation was a genuine risk.

Since the problem of free-riding cannot be ignored, the problem of dividing the cake must have been more challenging than Tomasello thinks. Nonetheless, his critics are in broad agreement that mutualistic collaboration in the context of collaborative defence, scavenging and hunting (and perhaps child-rearing) must have been key to the evolution of fairness concerns. Sterelny ([2012], [unpublished]) has suggested that instead of being supported by high-level social cognition, early forms of norm-based collaboration were supported by a suite of affective and retributive emotions.[9] These would not have provided the shortcut to the fully fledged norms of deservingness that Tomasello is concerned with, but they could have furnished hominins with less rigid and explicit (proto-)fairness concerns. These would have sufficed at the time, for there is an obvious default answer to the question what counts as a fair division in small groups with little to no division of labour: divide the cake in equal pieces.

5.2 Markets and the reciprocation crisis

If the task of dividing resources fairly was manageable in early hominin environments of cooperation, it certainly became strained later on. Tomasello sees the challenge of Late Pleistocene cooperation essentially as one of an expanding demographic scale. As groups grew in size, opportunities for collaboration scaled up in a manner that 'was relatively straightforward:

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[9] Perhaps the capacity for moralized norm-guidance was also rooted in skilled action, drawing on a pre-existing ability to recognize and follow non-social norms (Birch [unpublished]).

everything went from dyadic and local to universal' (Tomasello [2016], p. 86). The cognitive capacities for managing and maintaining cooperative relationships with single partners became adapted to dealing with relative strangers: the psychology of dyadic, joint intentionality evolved into one of 'group-minded', collective intentionality: 'There was [...] a transition from seeing an equivalence between oneself and one's collaborative partner, as did early humans, to seeing an equivalence among all who would be a member of the cultural group, that is to say, all rational beings' ([2016], p. 93).

Given the implausibility of the hypothesized baseline of joint intentionality, we already have good reasons to be sceptical about this solution to the challenge of Late Pleistocene cooperation. But, more importantly, we should question whether Tomasello's diagnosis of the challenge as one of an increasing demographic scale is correct. Again, Sterelny ([2014], [unpublished]) has argued convincingly that Tomasello underestimates the problem of Late Pleistocene cooperation. He points out that increase in group size must have been accompanied by diversification of the resource- and skill-set, as well as by shifts in the spatiotemporal scale of cooperation. Together, these changes constituted an important shift in the economic basis of cooperation. Food was no longer predominantly hunted by individuals that divided spoils on the spot and that could recognize each other as equally deserving based on their equal contributions. Increasingly, supplies became harvested by smaller parties, with different skill-sets and different degrees of success, who exchanged a variety of items in different quantities and at different rates. Cooperation based on collaboration with immediate returns gradually gave way to cooperation based on exchange with delayed returns. This transition introduced new risks of escalating conflict. Late Pleistocene hominins faced something of a 'reciprocation crisis' (Sterelny [2014], [forthcoming], Chapter 2, [unpublished]); they lacked the information needed to put themselves into their partners' shoes. The expanding resource base introduced issues of weighing effort, skill, and scarcity. What is a fair exchange of one's skilfully hunted, hard-to-catch, perishable gazelle for the heavy stones that a few others have carried (with little skill but much effort) from a well-known site? Such problems of incommensurability were compounded by problems related to the expanding time horizons of cooperation. Delayed and uncertain returns on investment introduced problems of agreeing on appropriate temporal discount rates for different transactions (Sterelny [2014], [unpublished]).

Sterelny's diagnosis of a Late Pleistocene reciprocation crisis is convincing. But I will argue that the solution he sketches does not fully address the problem. Sterelny ([2014], p. 74) hypothesizes that reciprocation-based cooperation was sustained and stabilized by 'shared, coordinated activity, as in ritual, ceremony, song, and dance' of which traces appear in the archaeological record from around 120 kya. The idea is that ritual activity would have

smoothed over tensions about exchange by reinforcing longer-term social bonds. Affiliative bonding facilitated exchange without being about exchange, but rather by being about the individuals involved in the exchange. Frictions that arose in the day-to-day activity of exchange were dampened and deescalated by restoring social relationships in the quiet hours. Sterelny ([2014], p. 74) suggests that ritualized peace-making activities of this sort could have provided a platform for agreeing on default norms of division: 'being in the same initiation cohort (for example) might link individuals firmly enough to maintain cooperative defaults [. . .] default expectations about (say) what kinds of product should be shared, and how the shares should be divided'.

Sterelny mentions Lamalera whale hunting in Indonesia as an illustration. The Lamalera have an elaborate system of distribution norms that specify which part of a sperm whale is to go to which party. The system includes norms about parties that were involved in very indirect ways, such as the sail maker and the craftsmen (Alvard and Nolin [2002]). But whale hunting with elaborate task division is not an exemplar of the main challenges posed by reciprocation-based cooperation. Although whaling involves considerable delays (and frequent failures) in return on investment—and hence does not qualify as an example of immediate-return mutualism—Lamalera whale hunting is more akin to Mid-Pleistocene game hunting than to Late Pleistocene reciprocation and trade. The stable task division and the large share of local, group-based activity preserves transparency in monitoring contributions made and benefits received. The problem space for determining a fair division is therefore relatively well-defined compared to cases of delayed exchange with a growing resource portfolio.

Take the question of how much meat I deserve from you today in return for the fish I gave you last week. It will not receive a satisfactory answer if the need and availability of both resources can change quickly and unpredictably. Droughts, resource depletion, luck, and the (relative) number of resource providers can change in ways that make a good deal today seems like a bad one in a few weeks. The possibility for convergence on default norms is thus eroded by the temporally shifting nature of the problem. Recurring patterns of change such as seasonal fluctuations could in principle be covered by series of default norms, but this quickly becomes too demanding in combination with other (individually predictable) dimensions of change that range over different timespans. To the extent that default norms of exchange fail to adjust to fluctuations, they will increase tensions in trade rather than reduce them. The disadvantaged won't recognize the norm as being about fairness and will be inclined to reject it. Hence, default norms neither enable nor sustain the challenges that are typical of the reciprocation crisis; they work for collaboration, but not for exchange.

If default norms were not the solution, what did stabilize economies of exchange? If, as I have argued, fluctuations in supply and demand were the key problem, the simplest solution would have been to account for those fluctuations. That is, a shared recognition that shifts in supply and demand should be reflected in the ratio of exchanged goods and services might have stabilized exchange-based economies. It could have prevented those economies from collapsing under the weight of accumulating grudges about unfairness among trading partners. However, as we saw in Section 4, reliably monitoring changes in supply and demand for a number of different commodities is a non-trivial task. Why think that Late Pleistocene hominins could have pulled off something that I took to be a problem for hominins on Baumard *et al.*'s account?

There are several differences between the account of Baumard and colleagues and the one I am starting from that make the idea of biological market effects less problematic and more promising in the present context. First, note that I am suggesting a role for biological markets late in hominin evolution. By this time, hominins had already evolved considerably more advanced cognitive and motivational capacities than on Baumard *et al.*'s account of biological markets, which goes back to (at least) our common ancestor with great apes. Thus, on my picture, biological markets did not select for enhanced memory, mind-reading, and social monitoring abilities, but took off from a point where these were already in place; they had evolved from the antecedent demands of collaborative hunting and caring. Second, the Late Pleistocene trading environment was more structured and localized than that of the primate baseline that Baumard *et al.* calibrate hominin markets to. It is likely that in the Late Pleistocene resources were transported to and exchanged at central camp or feeding sites, which provided some information about the local state of supply and demand. Hypotheses of (non-human) primate biological markets instead have to work with demographically scattered and changing sites of exchange. Finally, I am not proposing that Late Pleistocene hominins traded resources in complex configurations and kept track of complex supply-and-demand interactions between different combinations of commodities. As I argued in Section 3, such complex markets would have surely been out of reach in the absence of robust price mechanisms and bookkeeping methods. But we can imagine simpler forms of market-based trade where only certain pairs of resources are traded and where some resources are traded serially rather than in many (parallel) combinations.

Adrian Jaeggi and colleagues have recently shown that market-based dynamics of this sort play an important role in exchange-based cooperation in the Tsimane' forager-horticulturalists of lowland Bolivia. In a comparison of exchanges across five commodity classes—meat, (garden) produce, labour, childcare, and sickcare—they showed that 'some household-specific

cooperation strategies were consistent with market forces, that is, the costs and benefits of giving and receiving given their own and others' supply and demand' (Jaeggi *et al.* [2016], p. 5). Importantly, they also found that the Tsimane' do not trade all resources for each other, but only exchange them in particular, linked commodity pairs. Hence, their economy is fully connected, but not complex and web-like in structure. Another interesting feature of the Tsimane' exchange economy is that most trades are between varieties of material capital (meat for garden produce) or forms of social capital (labour for childcare, childcare for sick care) (Macfarlan [2016]). This suggests a (partial) solution to role- and resource-incommensurability problem: in the main, only similar forms of wealth are traded for each other, making it easier to compare resources and agree on exchange rates.

The Tsimane' aren't a perfect model for Late Pleistocene hunter-gatherers overall, but they are relevantly similar for our purposes. Since they live in relative independence from the larger Bolivian institutional-political system, they run an economy that is not governed by institutions and a judicial system that can enforce contracts. Their markets are much closer the biological, non-monetary bartering model than those of modern economic theory. If the reciprocation crisis constituted a real challenge, a restricted market-based economy similar in kind to that of the Tsimane' might well have been part of the solution.

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