The nutrient exchange mutualism between arbuscular mycorrhizal fungi (AMFs) and their host plants qualifies as a biological market, but several complications have hindered its appropriate use. First, fungal ‘trading agents’ are hard to identify because AMFs are potentially heterokaryotic, that is, they may contain large numbers of polymorphic nuclei. This means it is difficult to define and study a fungal ‘individual’ acting as an independent agent with a specific trading strategy. Second, because nutrient exchanges occur via communal structures (arbuscules), this temporarily reduces outbidding competition and transaction costs and hence resembles exchanges among divisions of firms, rather than traditional trade on markets. We discuss how fungal nuclei may coordinate their trading strategies, but nevertheless retain some independence, similar to human co-operatives (co-ops).

**Mutualisms as Markets**

Interspecific cooperative interactions underpin ecosystem stability and global nutrient cycles and provide a power driver for evolutionary innovation. Biological market theory (BMT; Box 1) provides a conceptual framework for analysing such cooperative exchanges that allow organisms to trade (see Glossary) goods and services in ways that potentially provide an advantage across changing contexts. BMT emphasises the central role of choice among partners that enact different trading strategies, varying in the quality or quantity of resources they provide. Partner choice has consequences over different time scales, notably, (i) selection for more profitable characteristics of trading partners over evolutionary time dimensions and (ii) ad hoc adjustments to changes in supply-demand ratios resulting from outbidding competition among individuals striving to increase their chances of being chosen [1–4]. When applied correctly, BMT allows formulating testable predictions about the variation in patterns of exchanges of goods and services across individuals and ecosystems.

Historically, BMT was inspired by empirical evidence arising from cooperation in animals. Market-like exchanges have been reported not only among members of the same species, for example, primates including humans [5–9], hyenas [10], and various cooperative breeders [11–13], but also between members of different species, for example, cleaner wrasses–fish clients [14,15] and ants–homopterans [16,17]. In all these ‘biological markets’, members of typically two different classes of traders exchange commodities, for example, female primates groom reluctant mothers to gain permission to interact with their newborns [18–20], cleaner wrasses feed on the ectoparasites of other fish [14], and ants protect aphids and caterpillars in exchange for carbohydrates [16,17].

Market-like exchanges involving non-animal partners have subsequently been reported as well, for example, ants offering protection to plants in exchange for nutrients and housing [21] and plants and microbes exchanging various nutrients ([22] and references therein). However, several misunderstandings have hampered BMT’s appropriate use in the latter case [23]. This is partially due to the problem of identifying the equivalents of independently acting traders and
key phenomena, such as partner choice and outbidding competition, which gets harder the further one moves away from the vertebrates in the tree of life. Without (i) the recognition of equivalent phenomena in otherwise disparate biological systems and (ii) agreement over the use of universal terminology, we may miss a great opportunity to develop universal models of the trade-like exchanges among organisms.

All major transitions in evolution have been possible thanks to the emergence and stabilisation of some form of cooperation [24]. One such major transition was the colonisation of dry land by plants via the aid of arbuscular mycorrhizal fungi (AMFs) and other mycorrhiza-like associations [25]. There is an increasing appreciation for the immense role of mycorrhizae, and microbes in general, as key nutrient exchange vectors, engaging in resource trade within and between species. While we are rapidly advancing in our ability to characterise microbial diversity, a larger understanding of the resources and services they exchange is lacking. In the case of the AMF–plant partnership, however, we are beginning to gain a clearer picture of the mechanisms behind mutual partner choice and commodity exchanges. This makes it suitable for testing whether a BMT vantage point helps to improve our understanding of plant–microbe interactions in general. We focus specifically on distinguishing the entities that act as trading partners and the mechanisms of partner choice.

In nature, the hyphae of AMFs and plant roots form vast underground networks that interconnect large numbers of individuals of both trader types, usually involving multiple species of both AMFs and plants. The term ‘network’ can be interpreted in two ways here. First, as the physical nutrient transport system consisting of plant roots and fungal hyphae, as often seen in the mycorrhizal literature (Figure 1A). Second, in terms of graph theory, as a bipartite network with two distinct sets of vertices: plants producing carbohydrates through photosynthesis and fungi extracting nutrients from the soil (Figure 1B), notably phosphorus and nitrogen (Box 2). The latter describes a market with two distinct trader classes accurately.

**Box 1. General Features of Biological Markets**

Even though atypical in some respects, nutrient trading between plants and arbuscular mycorrhizal fungi shows core properties of biological markets. These include the following [2,3]:

1. Commodities (goods and/or services) are exchanged between agents that differ in the degree of control over these commodities, which allows the distinction of two (or more) trader classes. Flowering plants and pollinating insects form an example.
2. The members of at least one class can choose their trading partners from many potential candidates. Choice can be reciprocal.
3. The relative value of a partner can either be judged directly on the basis of the utility of the commodities offered to the choosing agent, or indirectly on the basis of 'cues' (advertisements) that correlate with the commodities and their value. The petal disc of a flower is an example of an advertisement for the nectar it offers. As in commercial advertisements, there is a potential for false information.
4. There is competition among the members of the chosen class to be selected by the members of the choosing class. In principle, competitors can be excluded by forceful means, but the typical market dynamics emerge when agents compete by ‘outbidding’, that is, increase their relative attractiveness by augmenting the exchange value of the commodities they offer. This can either be done by increasing the quality and/or quantity of the commodity offered and/or by reducing the quality and/or quality of the commodity demanded in exchange.
5. Preference for the best offers causes supply and demand to determine the bartering value of commodities exchanged. For example: cleaner wrasses, small fish that remove and eat the ectoparasites of bigger fish, wait for their clients at a ‘cleaning station’. Clients that can visit multiple stations get better service than clients that have access to a single cleaner only [14].

Obviously, there is endless variation in the forms human economic markets can take, and no biological market is a faithful copy of any specific human market. Most human markets make use of a common currency and transactions are often secured by some form of binding contract, in contrast to biological markets [see 39] for exceptions]. Terms such as market, firm, and ‘co-op’ should primarily be seen as metaphors that help to conceptualize complex biological systems, suggest hypotheses and predictions, and serve as guides to the relevant economic literature.

**Glossary**

**Abortion**: in the context of mutualisms and symbioses between plants and other organisms, the abscission of parts of plants that contain one or more partners, resulting in their demise; specifically, the abscission of flowers and fruits that contain the larvae of "obligate nursery pollinators" such as fig wasps and yucca moths.

**Common (public) good**: a commodity that is available to all members of a group, community, population, etc. Defined in a strict sense a ‘public good’ is ‘non-rivalrous’, that is, the consumption by one agent does not diminish the amount available to another agent (e.g., a public radio broadcast). Usually called a ‘common good’ or ‘common pool resource’ when utilisation by an agent prevents its consumption by others (e.g., parking space).

Definitions vary among disciplines, however.

**Co-op**: abbreviation of co-operative; an association of traders that produce the same or exchangeable commodities and that cooperate to reduce the costs of (outbidding) competition.

**Cooperation**: mutually beneficial interaction between two or more individuals. Defined in a strict sense, cooperation is used when these individuals are members of the same species and mutualism is used when they belong to different species.

**Firm**: institution created to produce commodities in-house that would otherwise have to be purchased on the open market at additional costs, the transaction costs. Can be understood as the antonym of 'market' [38].

**Market**: institution that allows the exchange of commodities among independent agents (traders). On biological markets, commodities are exchanged directly at exchange rates coupled to supply-demand ratios through processes such as partner choice and outbidding competition.

**Mutualism**: mutually beneficial interaction between members of different species. Conceptually equivalent to cooperation between unrelated members of the same species.

**Outbidding competition**: competition over access to (potential...
The Key Role of Partner Choice in BMT
BMT was primarily motivated by the lack of appreciation for the role of partner choice in models of the evolution of cooperation among unrelated agents [1–3]. Partner choice, which includes all forms of discrimination between potential and actual cooperative partners, can have consequences at an ‘ecological time scale’, spanning a single generation and at an ‘evolutionary time scale’ spanning numerous generations. Over their lifetime, individual agents can adjust partners by offering higher benefits to those partners in the form of lower prices or exchange rates, or by offering commodities of better quality.

Price: can be expressed in a common currency if one exists on a market (e.g., fiat money), but on biological markets without currencies the price of a commodity X is expressed as an ‘exchange rate’: the number of units of the commodity Y against which one unit of X is traded.

Punishment: one of several options open to agents that consider themselves cheated or short-changed by a partner. Punishments are attempts to change the future behaviour of the punished to the advantage of the punisher and usually occur in between consecutive cooperative or mutualistic interactions.

Sanction: cutting off the flow of a resource that is exchanged in the context of mutualistic trade. A term specifically used in the context of partnerships between large, multicellular hosts and their microbial symbionts. Sanctioning normally results in the demise of the sanctioned partners, which makes it conceptually similar to abortion.

Social dilemma: a conflict between the selfish interest of an individual agent and the communal interest of the group to which the agent belongs. (Not) paying taxes is one of an infinite number of examples.

Trade: the exchange between two agents of one commodity, either a good or a service, against another.

Trading strategy: a conditional strategy (sensu game theory) that prescribes trading behaviour under all circumstances regularly encountered by members of the trading agent’s species. Trading strategies of non-cognitive agents, such as plants and fungi, are assumed to be shaped exclusively by natural selection.

Trader: any agent capable of independently implementing a trading strategy. Trading agents such as firms, co-ops, federations, and unions may comprise multiple individuals.

Transaction costs: any costs related to trading on a market apart from the production costs of the commodity offered itself, for

Box 2. AMFs
Species of arbuscular mycorrhizal fungi (AMFs) interact with 80–90% of terrestrial plants, many of great agricultural importance [77,78]. These plant–fungus associations, with evolutionary origins dating back roughly 450 million years, mediate nutrient cycles and energy flow through terrestrial ecosystems to a large extent. Individual plants tend to be connected to multiple strains and species of AMF [68], trading 4–22% of their assimilated carbon for phosphorus and nitrogen [46,79]. Plants can take up nutrients directly from the soil, but trade with far-reaching fungi is often favourable because nutrients are quickly depleted around the roots. AMFs penetrate host cells where they form tree-like structures, called arbuscules. These are the primary sites of nutrient transfer. How long an individual arbuscule persists (about 4–10 days) is probably due to an active choice of the plant host, whereby less beneficial arbuscules degenerate faster than more profitable arbuscules [46,57,58].

AMF mycelia grow from single spores containing large numbers of nuclei. The nuclei multiply in the growing mycelium, which consists of aseptate hyphae, that is, the nuclei can move freely. Nuclei can also migrate from one individual to another during anastomose, the fusion of hyphae [34]. The genetic variability of the nuclei within a single AMF is a hotly debated issue. Some argue for a clonal state of the nuclei (homokaryosis), while others support the idea that there are large numbers of genetically different nuclei (heterokaryosis) [14,30–33]. This debate is closely linked to another debate: the sexual reproduction of AMFs. Unambiguous fungal sex has never been observed, but there are indirect indications of cryptic sex and genes associated with meiosis [35,80,81].
their trading strategies to spatial and/or temporary changes in the supply and demand of the commodities they trade. Such behavioural, physiological, or morphological adjustments may be in response, for example, to changes in the numbers of competitors, an influx of a certain nutrient, or seasonal effects. These instant adjustments to supply-demand ratios are reminiscent of human ‘economic’ behaviour and have historically attracted most attention from those interested in biological markets.

Consistent partner choice for certain trait values in partners should also have evolutionary consequences, however. Because of the preferences of the members of one trader class, the characteristics of the members of the chosen class can change from generation to generation. The mechanism is not unlike the selection of the peacock’s train due to the preferences of females, except that ‘market selection’ often results in quite less spectacular traits, for example, the dull plumage of subordinate male birds [26] or the production of additional sugars as rewards for protection, pollen transport, or nutrients [14].

Using a market framework for mycorrhizal mutualisms forces a balanced look at partner choice at both time scales, and also across both sides of the partnership, rather than taking the traditional plant-centred vantage point. The use of terms such as ‘ineffective’ or ‘inefficient’ with reference to AMFs, for example, betrays an agricultural, rather than biological, focus. An inefficient transaction from the point of view of the plant can be highly efficient for its fungal partner. ‘Profitable’ would be the preferred market jargon, and all attempts should be made to quantify this as a net benefit relative to alternative sources of the same nutrient.

### Identifying Trading Partners

For biological markets with vertebrate actors, the concepts ‘trader’ and ‘individual’ coincide: each trader/individual is assumed to act as an independent agent executing evolved ‘trading strategies’ adapted to the kind of market in which they typically find themselves. This assumption follows the canon of individual selection, which has been theoretical orthodoxy ever since George William’s classic marked the demise of naïve forms of group selection [27]. The individual can be conceptualised as a package of cooperating genes that float or sink together.

But what if trader does not coincide with individual? How are traders identified, for example, when members of an eusocial ant colony protect clonal groups of aphids in return for the honeydew [16]? What is the equivalent of a trader, the individual aphids and ants or the aphid clone and the ant colony? What if the ant colony was founded by multiple unrelated queens [28]? Put differently: at which level of adaptation (sensu [29]) do we find the agents that implement trading strategies independent from other agents in their trader class, and then pass these strategies on to the next generation of traders?

The problem of identifying traders is brought to yet another level of complexity in the plant–AMF mutualism. Identifying a plant individual can be difficult when dealing with clonal plant groves connected by ‘single’ root systems, which in some cases can reach ~0.5 km² (e.g., *Populus tremuloides*). Identifying a mycorrhizal fungal individual acting as an independent agent is even more of a challenge.

An AMF mycelium germinates from a single spore. There is evidence that spores can be heterokaryotic, that is, may contain several hundred nuclei of different genetic composition [30], but whether this is indeed the case and if so, how different, is a matter of debate [31–33]. Hyphae of closely related fungal strains can also fuse (anastomose) and share nuclei [34]. As the hyphae are aseptate, that is, have no internal septal walls, nuclei can potentially move across
the entire hyphal network. Thus, at all stages, AMF mycelia may bear multiple genomes. This raises important questions about a core element of any biological market: reciprocal partner choice. (i) If plants discriminate among mycorrhizal partners, from which components of the fungi are they choosing? Put differently: can we determine the essential carrier of the genetic information that determines those fungal trading strategies that are passed on to the next generation? (ii) Conversely, assuming AMFs choose their partners, too, which component of the fungus discriminates among various plant partners?

In practical terms, we can build models with individual plants as independently trading agents, given certain caveats, but we have to tread more carefully in the case of the fungi. Given the current debate surrounding the genetic structure of AMFs [31,33,35], we consider the consequences of homokaryosis (all nuclei in both spores and the mycelium are identical) and heterokaryosis (a large variety of genetically different nuclei) alongside each other (Figure 2). Dikaryosis (two types of genetically heterogeneous nuclei) is another valid possibility [32], but the difference with heterokaryosis has no fundamental repercussions for our argument. Below, we discuss the key attributes that define traders, including the use of conditional trading strategies and traders forming temporary firms.

**Figure 2. Potential Discrimination Mechanisms.** The two rows of this table reflect the two karyotic states of AMFs most often mentioned in the literature: homokaryosis and heterokaryosis. The two columns reflect two hypotheses about the mechanisms by which discrimination of plants among individual arbuscules would result in selection among either fungal individuals or individual nuclei. The Limpens and Geurts hypothesis depicted in the left column was originally proposed by Limpens and Geurts [56] for heterokaryotic fungi only (bottom row), but here we illustrate its (lack of) consequences in the case of homokaryosis, too. According to this hypothesis, nuclei coding for less profitable trade (black) would be less likely to end up in spores, because plants “sanction” the arbuscules associated with these nuclei. According to the metabolic rate hypothesis (right column), plants would preferably allocate carbon to arbuscules with more profitable exchange rates, the ones governed by a majority of profitable (red) nuclei, that would lead to higher local metabolic rates, resulting in local proliferation of hyphae and higher rates of mitosis of nuclei and spore formation. The resulting four panels depict the scenarios that result when the two choice mechanisms are combined with the two karyotic states. Choice by the plant host at the level of individual arbuscules can change the ratio of profitable and less profitable nuclei when the sets of nuclei associated with individual arbuscules differ in their genetic composition, that is, heterokaryosis (bottom row). In the case of homokaryosis (top row) discrimination by plants can only have a selective effect at the level of complete AMF–mycelia because of a lack of intra-individual genetic variation, that is, an eventual link between arbuscular degeneration and spore formation does not play a role.
Traders Use Trading Strategies
Trading strategies are conditional strategies shaped by natural selection; they resemble algorithms that prescribe the actor which actions to take under which conditions. Trading strategies can vary from species to species and also among members of the same species. The most profitable partner in one type of environment is not necessarily the best partner in another. Some prefer describing this as ‘adaptive phenotypic plasticity’, but there are at least 11 different definitions of plasticity, resulting in a rather heterogeneous literature [36]. We therefore prefer the more accurate language of game-theory [37].

The Market–Firm Dichotomy
The formation of new or alternative partnerships has sizeable costs, including costs of searching for partners and comparing offers and opportunity costs due to time lost and suboptimal partners, and so forth. These costs of trading on markets, known as ‘transaction costs’ in economics, can either be avoided by the formation of ‘firms’ that allow in-house production of a commodity or be limited by concluding long-term ‘binding contracts’ with fixed suppliers [38].

Recognizing the biological equivalent of the firm versus market dichotomy guides us to a large literature in economics [39]. The distinction between vertical and horizontal transmission of symbionts provides a valid example [40]: vertically transmitted symbionts form a firm with their hosts, in which symbiont genotypes are passed down through generations of hosts. In contrast, hosts that acquire their horizontally transmitted symbionts on a ‘market’ must search for new symbionts at least once per generation. AMFs are not vertically transmitted, but the plant–fungus relationship can last a long time, even though the structures where the actual trade takes place, the arbuscules, have a high turnover. The necessary spatial proximity and investment in communal structures make partner switching costly, but both plants and AMFs usually have contacts with multiple partners simultaneously. Thus, nutrient swaps between plants and mycorrhiza fall somewhere between exchanges among divisions of the same firm and acquisitions on open markets. Firms are formed temporarily, alternated by phases of market trading.

Putting Partner Choice into Effect
Partner choice is what makes (biological) markets tick [1,2,5,14]. Without partner choice, there is no outbidding competition among the potential partners and hence no adjustment of prices, that is, exchange rates of the commodities traded, to shifts in supply and demand. Evidence of partner choice therefore is the litmus test for the potential presence of market mechanisms. The observation of nutrient exchanges alone does not suffice to show that market dynamics are at work [4]. It is thus crucial to agree what we call partner choice in the context of underground nutrient exchanges.

Some only consider an expression of partner preference before actual nutrients are being exchanged as true partner choice ([41], and references therein); others distinguish pre-trade partner choice, preferential allocation, and sanctioning as fundamentally different mechanisms [42,43]; and yet others consider all forms of partner discrimination at any stage as partner choice, in line with the tradition in BMT-based research [44]. We propose using partner choice as an overarching term that includes any form of discrimination among actual and potential partners at any stage of the interaction, since BMT is informed by economics and hence defines partner choice in the spirit of human markets. Take labour markets: employers choose their employees by hiring and firing but also by promotions and demotions as well as by increasing or decreasing their salaries. It is the whole spectrum of partner discrimination that counts, not just the first instance of partner selection.
A Classification of Partner Choice Mechanisms for Mycorrhizal Markets

For mycorrhizal mutualisms, one can theoretically distinguish three modes of partner choice: (i) potential partners are chosen based on cues, signals, or advertisements before any nutrients are exchanged; (ii) nutrients are allocated to more profitable partners and withheld from others during ongoing trade with multiple partners; and (iii) trade is ended with some partners, but not with others.

Choice before Nutrients Are Exchanged

A considerable amount of mutual signalling indeed takes place before the fungal hyphae actually penetrate the root [45,46]. This may imply a preliminary choice at the species level but is less likely to be a choice at the individual level as this would require ‘honest advertisements’ rather than signals or cues [47,48] (Box 3).

Choice during Trade versus Ending Trade

‘Sanctioning’ and ‘punishing’ are two terms frequently used in connection with underground partner choice. In this context a distinction is often made between ‘hosts’ and ‘symbionts’, whereby the hosts are assumed to be in control. Hosts can sanction less profitable symbionts, for example, by cutting them off from nutrients, which will affect the symbionts’ fitness [49]. Sanctioning is conceptually similar to the abortion by plants, such as figs, yuccas, senita palms, and several others, of fruits and flowers that are too heavily claimed by ‘nursery pollinators’ [50–52].

Lethal trade termination can have strong selective effects and hence result in more beneficial partners over evolutionary time, but it obviously cannot incite individual partners to yield more immediate net benefit [53]. It may select for more profitable partners for the host’s descendants, but why such mechanisms evolve in host species is not obvious, since the ‘improved’ symbionts constitute a common good for future generations and the usual caveats of social

Box 3. A Classification of Criteria on Which Partners Can Be Chosen

Signals and Advertisements

Signals are (i) specifically evolved to improve the chances of being chosen, (ii) are not part of the commodities eventually traded, and (iii) play no role after actual trading has started [48]. Selection for signalling is only likely when signals are considerably cheaper to produce than the commodities actually traded and/or reach more potential partners. Advertisements form a special sub-category: they convey additional information about individual quality. Species-specific signals can be used to discriminate between mutualistic and non-mutualistic species, but individual-specific advertisements can be used to discriminate among competing traders belonging to the same species. The ‘honesty’ of advertisements is a major issue in biological markets [47].

Cues

Cues provide useful information about the identity and quality of the chosen party, but do not require any specific investment, for example, byproducts of basic metabolism leaking into the environment. Cues benefit the receiver exclusively and receiver-specific adaptations evolve to respond to their presence (for the difference between cues and signals, see [48]).

Nutrients

The decision to increase, decrease or end trade, respectively, can be based on (i) the quality and/or quantity of nutrients received only; (ii) the exchange rate, that is, the minimum amount to be delivered to ensure the receipt of the minimum amount required; or (iii) the net gain per unit time. This classification may seem like hair splitting, but the different parameters suggest different physiological mechanisms. Which one is actually used will depend to a large extent on what the two trading parties can reliably measure.
dilemmas apply [54]. Selection can only result in the costly production of such a common good when at least one of two conditions is fulfilled: (i) The sanctioning host’s immediate descendants are more likely than any other traders to interact with the more profitable symbionts. This would be the case when symbionts are vertically transmitted. (ii) The host’s generation time is much longer than that of its symbionts, such that the host itself profits from more beneficial generations of symbionts. Neither condition is fulfilled in the plant–AMF mutualism.

An alternative explanation, which applies notably to abortion, is that eliminating less profitable symbionts is a byproduct of mechanisms with other functions. Most plants will drop flowers and fruits if they have been damaged, rot, or are infested by parasites, because this directly benefits the aborting individual. Similar pre-adaptations may have played a role in plant–microbe interactions too. Plants may sanction microbes by shutting down nutrient flows, but the term ‘abortion’ would be appropriate when parts of the root structure containing less profitable partners are sacrificed.

**Punishments should incite partners to ‘behave better’ in the near future and therefore are non-lethal by definition** [55]. What punishment by plants actually entails is not as obvious as, for example, client fish chasing biting cleaners [14]. If hosts recruit symbionts from a common pool of symbionts, then punishing is a costly investment in a collective action producing a common good and hence unlikely to evolve for the same reasons as mentioned for sanctioning above. Punishment can evolve if the symbionts are committed to the punishing partner, for example, by lack of mobility or while switching hosts is prohibitively costly.

**How Could Plants Select for More Profitable AMFs?**

How could partner choice by plants drive selection for more profitable fungal partners, given that sexual reproduction is potentially absent, or at best cryptic, in AMFs and that they contain large numbers of nuclei that may or may not be identical (Box 2)? When all nuclei of an individual AMF are identical (homokaryosis), partner choice by plants can only have a selective effect at the level of entire individuals, assuming that there is at least, due to some unknown cause, inter-individual genetic variation among those members of the same AMF species that are within reach of individual plants. When there is within-individual genetic variation (heterokaryosis, or eventually dikaryosis), however, plants may discriminate among nuclei as far as they cause the fungus to execute local trading strategies that differ in their profitability to the plant.

For the latter case, Limpens and Geurts [56] proposed a scenario that builds upon well-documented phenomena of exchange at the plant–fungal interface (Figure 2, column 1). Arbuscules, the intra-cellular nutrient exchange sites to which both plants and fungi contribute, persist for about 4–10 days, a considerably shorter time than that of the host cell [46,57]. This is puzzling, given that both partners lose investment. There is evidence that arbuscules degenerate sooner the lower their nutrient exchange rate is [58]. Limpens and Geurts’ crucial contribution is the hypothesis that nuclei associated with ‘beneficial’ arbuscules have a better chance of ending up in spores than those that are less profitable to the plant. This is supported by evidence that spores of the same fungal individual can potentially contain different sets of nuclei [59–62]. While spores can have visibly different morphologies, it is not clear how or what determines nuclear distribution.

We can also imagine an alternative scenario (Figure 2, column 2): a higher trade volume via an arbuscule could lead to a locally more active metabolism, accelerated local growth of hyphae, and increased mitotic activity, resulting in higher numbers of the associated fungal nuclei. Both
scenarios, which are purely hypothetical and not mutually exclusive, would lead to a higher relative frequency of nuclei programming for trading strategies that are beneficial to the plant.

While the mechanisms are as of yet unknown, it is clear that the genetic information determining trading strategies is neither likely to be uniform for the whole mycelium of an AMF nor vary locally under the influence of single nuclei. Strategies are more likely associated with something in between: subsets of nuclei. We propose to use the term ‘co-op’, the abbreviation of co-operative, for this intermediate type of trading entity. In human societies, co-ops are formed to reduce competition among actors producing the same commodity without giving up independence completely.

According to the Third Rochdale principle, a loosely defined set of rules for the organisation of co-ops, surpluses are partly reinvested in the co-op and partially benefit the co-op’s members, specifically in proportion to their share in the production of the commodities sold on the market [63]. At which level of organisation fungi trade is largely an empirical question. An AMF is best considered as a single trader if it contains a homokaryotic genetic structure. If, however, plants effectively choose among subsets of genetically diverse nuclei by discriminating at the level of individual arbuscules, for which there is some empirical evidence [58], then groups of nuclei linked to those arbuscules are better compared to co-ops of traders. These would be short lived, and co-op membership would be partially reshuffled from generation to generation, something loosely comparable to recombination.

Switching Partners
Adjustments to varying supply-demand ratios are notably driven by partner switching. Two forms can be distinguished. In a hard switch, a trader replaces one trading partner with another. In a soft switch, the actor remains connected to multiple trading partners but shifts resources from one partner to another, effectively playing partners against each other continuously. Monitoring nutrient flows may have some costs, but search costs have to be paid only when new partnerships are formed. Soft partner switching, which has been labelled ‘(dynamic) preferential allocation’ [42,43], is likely to be prevailing on plant–AMF markets.

Optimal Number and Composition of Partnerships
Trading with multiple partners has two main advantages. First, it induces outbidding competition and second, it is a form of bet-hedging. There are fallback options if a partner stops trading or is lost due to pathogens, herbivores, or other causes. Bet-hedging may partially explain why plants that invest more in mycorrhizal trade do not consistently receive more in return [64] and why fungi connect to plants of different species, ages, and nutrient statuses, including low-quality hosts [65]. The question is not only how to select the most profitable partners but also how to arrive at the optimal number of partners, at the right mix of different kinds of trading partners, and at the right investment in each of them. One recent model predicts ‘linear proportional discrimination’: each trader allocates resources to its partners in proportion to the relative amount of benefits it receives from them [66], but experimental work is needed to test this.

Experimental Evidence of Partner Choice
There is evidence that both plants and fungi can exert partner choice: they are able to detect variation in nutrient provisioning by their partners and react by favouring exchanges with more profitable partners (reviewed in [22,67,68–72]) (Box 4). In principle, partner choice will have a selective effect on trading strategies, unless there is no variation left to choose from. When partner choice mechanisms are no longer used, they may be lost due to genetic drift or even
Box 4. Partner Choice Mechanisms in Mycorrhizal Markets

The accumulating evidence of reciprocal partner choice between plants and AMFs was recently reviewed elsewhere [82,83]. We give some empirical examples of mechanisms active during the initiation of trade and mechanisms active during ongoing trade, either to adjust or to end it.

Initiation of Trade

Both plants and AMFs are able to perceive information from nearby potential partners [46,58]. Plants, for example, produce strigolactones that couple environmental signalling (phosphorus availability) with symbiosis signalling (microbial recruitment), stimulating the AMFs’ hyphal branching. The fungi, in turn, generate lipo-chitooligosaccharides and chito-ligosaccharides that elicit pre-symbiosis responses of plants [46,84]. Whether this informs them of differences in potential profitability is less obvious.

Adjustment of Nutrient Flows

Whether and how plants and fungi can adapt their trading strategies over time and space remains a hot topic [42,74,75,85–89]. Plants can adjust trade with AMFs at a coarse scale through selective root growth and allocation of nutrients to specific root tips [88] and at a fine scale by allocating nutrients to specific parts of the fungal network [86]. Adding phosphate to the soil that can be taken up directly by the plant roots can also lead to a reduction of AMF colonisation of roots and reduce carbon flows to fungi [90–93].

Inversely, fungi can also adapt their offers, but mechanisms are less well known [71,94]. They can preferentially allocate phosphate to those root-sections providing more carbon [86,95] and more nitrogen and phosphorus to hosts in full sun than those shaded [85,96]. Plants also receive more phosphorus from a normally less beneficial strain when another AMF species is present, suggesting outbidding competition [97]. This confirms a mycorrhiza-specific model predicting that an increase in the number of mycorrhizal partners per plant increases both the cooperativeness of each mycorrhizal fungus and the fitness of each plant, and vice versa [96]. In some cases, the amount of carbon delivered by plants directly determines the amount of phosphorus received and vice versa [71,72,85,86,98–100]. This has, however, neither been consistently supported empirically nor is it required to support market theory [23]. Both evidence and theory also support the idea that AMF’s can reduce the capacity of plants to take up phosphorus directly from the soil, making plants more dependent on their trading partners [101].

directional selection when they are sufficiently costly to maintain. The ability to effectively choose partners may be preserved, however, for two reasons. (i) Conditional trading strategies, even when identical for all members of a species, may result in different offers under different environmental conditions [73]. (ii) Trade-relevant traits may differ between two species, even if they have gone into fixation in both of them. Many splinter root experiments with two different species of AMF are based on the second assumption [74,75]. A positive result shows that a species is able to choose and hence could potentially put selective pressure on its partners, but it does not show that it actually played such a role in the evolutionary history of either partner species. Plants may well prefer one fungal species over another and this is likely to have effects on the fungi’s local densities, but this preference will have no selective effect when there is no discrimination at level of individual fungi or their nuclei. A multi-generation design with choice among members of the same species is needed to prove actual selection [76].

Concluding Remarks

When describing the AMF–plant mutualism in economic terms, the identification of individual traders remains the major challenge. The solution we propose, if indeed the fungi are heterokaryotic, is to consider groups of fungal nuclei that determine a trading strategy together, and that are potentially chosen by their plant partners as a group on that basis, as co-ops. These groups of traders can potentially reduce competition among themselves and cooperate to a large extent but can also fine-tune their own trading strategies independently. Plants and fungi also potentially avoid paying the full transaction costs inherent to trading on markets, by forming long-lasting and intimate partnerships that can be compared to temporary firms. The comparison with traders on markets draws attention to the outside options both plants and fungi have.

Outstanding Questions

Questions Discussed in the Main Text
• How can traders, that is, agents with independent trading strategies, be identified?
• Is the market–firm dichotomy relevant to underground markets?
• On the basis of which characteristics is one partner preferred over another?
• How is partner choice implemented by either party?
• Do members of the same trading class compete with each other through outbidding?
• What is the optimum quantity and mix of partners?

Additional Questions
• Do plants and/or fungi stimulate outbidding competition among their partners and if so, how?
• Can either party actively play off its partners against each other by passing on information about alternative bids?

Plants are reported to communicate via mycorrhizal networks [102,103], but the same mechanisms could also help fungi playing off plants against each other [104].
• Is there competition among underground traders other than through outbidding?

We assumed competition by outbidding to be the main form of competition, but in the human and animal world, there obviously is an option to compete by force and chemical warfare, too. Do plants harm plants, or do fungi harm fungi to have less competition over mutualistic partners?
• Have ‘forced dependencies’ evolved in some mycorrhizal mutualisms?

An increase of the dependency on the partner species over evolutionary time can in principle come about in two ways: (i) For members of species A it is cheaper to purchase commodity X from members of species B than to produce it themselves. According to Ricardian’s comparative advantage principle, this can apply even if species A produces X cheaper than species B does [106–107]. (ii) Species B interferes in the genetic pathways and/or metabolism of the members of species A in such a way that the dependence of A-traders on the trade with B-traders increases [4,101].
Modelling mycorrhizal mutualisms as markets, on which both co-ops and firms are active, considerably extends basic biological market theory and allows more realistic models of mutualisms with temporarily or permanently cooperating traders, such as kin groups, eusocial and clonal organisms, symbioses, and so forth. Inversely, the possibility of manipulating both trader classes and quantifying nutrient flows, allows testing predictions in mycorrhizal mutualisms with an accuracy that is hard to achieve for other biological markets (see Outstanding Questions).

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