**PERSPECTIVE**

# Evolution of microbial markets

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Biological market theory has been used successfully to explain cooperative behavior in many animal species. Microbes also engage in cooperative behaviors, both with hosts and other microbes, that can be described in economic terms. However, a market approach is not traditionally used to analyze these interactions. Here, we extend the biological market framework to ask whether this theory is of use to evolutionary biologists studying microbes. We consider six economic strategies used by microbes to optimize their success in markets. We argue that an economic market framework is a useful tool to generate specific and interesting predictions about microbial interactions, including the evolution of partner discrimination, hoarding strategies, specialized versus diversified mutualistic services, and the role of spatial structures, such as flocks and consortia. There is untapped potential for studying the evolutionary dynamics of microbial systems. Market theory can help structure this potential by characterizing strategic investment of microbes across a diversity of conditions.

cooperation | mutualism | trade | partner choice

A perspective borrowed from another field of research often offers insights for generating new hypotheses and approaches (1). Biological market theory argues that exchanges of resources and services among organisms can be analyzed in market terms, with individuals making strategic trading investments to maximize market gains (2, 3). However, it is unknown how applicable the theory is across diverse systems or whether it can be of use to predict how cooperative strategies evolve.

One area where market theory is particularly useful is in the study of mutualisms: cooperative interactions between individuals of different species. A major question in mutualism research is why organisms provide benefits to other individuals at a potential cost to themselves. An important variable in maintaining mutualisms is the degree to which an individual can control the fitness of its partner (4). When both partners retain control and can actively choose whether or not to cooperate, exchange processes are more analogous to human markets because trade (leverage) operates over force (coercion) (5).

Mutualisms involving microbial partners are relatively underexplored because actions and responses can be harder to observe. However, every species on earth is involved directly or indirectly in one or more microbial partnerships; some are involved in hundreds (6). These interactions play an important role in animal and plant evolution, ecology, and development (7–9). Microbial mutualisms exhibit the same characteristics as other mutualisms, including competition among multiple partner lineages and a potential to cheat (10). An essential component of understanding these systems is determining what helps to stabilize cooperation between partners over evolutionary time. This is a large question, with answers that vary across mutualistic systems.

A market framework can theoretically be used to study mutualisms if the following conditions for biological markets are met (Box 1 and refs. 2 and 3): (*i*) commodities (goods or services) must be exchanged between individuals; (*ii*) at least two distinct classes of traders must exist; (*iii*) individuals from at least one trader class must be able to choose or switch partners; and (*iv*) there must be individual differences in commodity price so that there are opportunities for "outbidding" price competition. Additionally, most markets are also characterized by (*v*) temporal variation in supply and demand of the commodities, which can initiate price fluctuations (2, 3).

An important advantage of a market framework is that strategic investment on both sides of a mutualism can be studied (multiplayer models), while taking into account the biological context of the exchange, such as availability of partners or level of external resources. The emphasis is on the relative value of goods and services exchanged and how this value changes as the biological context changes. This includes potential situations where services or goods are of so little value that it is more beneficial to refrain from trade.

However, although the market analogy is appealing, empirical tests of the theory have focused on animal systems (e.g., refs. 20, 29, and 31; see Box 1 for more examples). This focus is a potential problem because we still do not understand how cognitive abilities contribute to the emergence of market dynamics (32, 33). Advocates of biological market theory argue that cognition is not needed and terms of trade can be explained solely by the current value of the potential partner and the context of the exchange (34). The expectation in market theory is on immediate rewards, not anticipated benefits:

## Box 1. Characteristics of biological markets

### (*i*) Exchange of commodities

The most basic element of any (biological) market is the exchange of commodities between two interacting partners. Commodities can be resources such as nutrients (11) and services such as grooming (12). In some primate species, mating opportunities are exchanged for grooming services (13, 14). Aphids exchange honeydew, a nutritious resource, for ant-protection services (15, 16). Although biological markets typically involve the exchange of different commodities, primate-grooming markets are an example in which the same commodity is provided by both partners (17, 18).

### (*ii*) Distinct classes of traders

Each biological market exchange requires two distinct classes of actors, or trader classes, both of which have a commodity to offer (2, 3). Trader classes can belong to the same species as in mating or cooperative breeding markets (13, 19) or to different species (mutualisms) (20, 21). In mutualistic biological markets, both trader classes have an advantage over the other class in producing and providing their specialized commodity (22, 23).

### (*iii*) Choosing and switching partners

In any market, trading partners are chosen from a number of potential partners. Individuals discriminate, choosing a partner based on differences in the price or quality of the commodity offered (24). Ants choose aphids producing the highest quality of honeydew and remunerate them with high-quality protection services (15, 25). Similarly, in primate-mating markets, males that offer more grooming are rewarded with more mating opportunities (13, 26). Such economic partner discrimination is the key factor driving market dynamics (24, 27) and distinguishes biological markets from traditional two-party, direct-reciprocity models (28). Therefore, only mutualisms that involve discrimination among partners by one or both trader classes can be considered biological markets.

### (*iv*) Price differences

Analogous to human markets, competition between individuals within a trading class can drive down commodity prices in so-called "outbidding competition" (3). In human economies, this idea manifests as "price wars." For instance, cleaner fish provide a higher-quality cleaning service in the presence of other competing cleaner fish (29, 30).

### (*v*) Supply and demand variation

Supply and demand determine the bartering value of commodities exchanged (2). Supply and demand are not fixed quantities but are inherently context-dependent and change over time. For instance, if more food-providing vervet monkeys are introduced in a population, the grooming services received as payment decrease (31).

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advantageous responses can evolve without cognition (35).

If biological markets do not require cognition, we predict that the theory can be effectively extended to organisms without nervous systems, like microbes. Have microbes evolved strategies that allow them to discriminate among trading partners? Do microbial mutualism markets follow the laws of supply and demand? Although some pioneering modeling work has been done in plant–microbial mutualisms (11, 22, 36, 37), these advances have been almost purely theoretical. However, technological advances, such as creating cheating mutants or artificially manipulating investment (e.g., ref. 38), now allow us to study cooperation, and more specifically market dynamics, in microbes (10).

In this Perspective, we explore the evolution of market strategies by microbes. We only consider systems in which at least one of the two trading partners is microbial. We discuss microbial market research questions, such as the evolution of microbial partner discrimination and the role of environmental variability on microbial cooperation, and propose methods to address these questions (Table 1). Experimental and theoretical study of such questions will drive forward our understanding of microbial markets and of microbial cooperation in general. This includes potential practical applications of microbial markets, for instance, in human health or sustainable agriculture (see *Applied Microbial Markets* below). We identify and discuss six economic strategies important for microbes to optimize their success in potential biological markets: (*i*) avoid bad trading partners; (*ii*) build local business ties; (*iii*) diversify or specialize; (*iv*) become indispensable; (*v*) save for a rainy day; and (*vi*) eliminate the competition. These strategies are not necessarily mutually exclusive: microbes may use multiple strategies and some microbial behaviors may correspond to aspects of more than one strategy. In some cases (e.g., becoming indispensable), it is the coevolution of partners promoting a market, not necessarily an active strategy driven by one side. Lastly, although the ability of at least one trader class to choose among competing partners is an important condition for markets to emerge, microbes can also use strategies that limit market choice in an effort to gain monopolistic control (strategies iv and vi). In all cases, strategies are selected because they benefit the individual microbe, or a co-occurring clone of identical microbes, not because they optimize the market as a whole: choices beneficial to individual traders can have the short-term effect of restricting options available to a trading partner. Even though such strategies can initially limit market dynamics, they might be restored when new competitors offering the same service enter the exchange.

## Microbial Market Strategies

**Strategy One: Avoid Bad Trading Partners.** Among the most important requirements for a biological market to emerge is for individuals to be able to discriminate among a variety of partners (Box 1, condition iii). Discrimination is the act of evaluating and comparing trading partners based on their actual (or perceived) contribution to an interaction (24). This is essential when individuals interact with multiple partners because it allows for simultaneous comparisons of quality among competitors. For instance, using a biological market framework, researchers have demonstrated how client fish will switch to better quality cleaners if they are cheated by a cleaner that feeds on their mucus or scales (20, 29, 30).

Experimental research in plant–microbe mutualisms has tested similar ideas, asking whether plant hosts can detect variation in resources or services provided and respond accordingly. Such discrimination mechanisms have been found in legumes, with some

**Table 1. Research questions relating to the evolution of microbial biological markets**

| Evolution of | Question | Suggested approaches |
|---|---|---|
| Variation in partner quality | What is individual variation in market prices? | Descriptive; study microbial individuality |
| | Is it influenced by level of competition? | Manipulate level of competition; study change in partner quality variation |
| | Can it be used in an applied way? | Identify best genotypes for systems useful to humans; use experimental evolution to generate variation |
| Partner discrimination | Can microbes simultaneously evaluate partners and discriminate? | Track nutrients in networks/aggregates of microbes interacting with multiple partners |
| | For free-living microbes, can (chemotactic) mobility achieve discrimination? | Choice experiments between high- and low-quality partners |
| | Is discrimination more likely in multicellular than in single-celled microbes? | Descriptive studies; compare occurrence of partner discrimination |
| | Does spatial structure promote discrimination? | Analyze preference for quality partners in consortia/biofilms vs. in free-living microbes |
| Markets under volatility | Do trading partners respond to resource volatility according to market hypotheses? | Manipulate resources; track effects on microbial trade |
| | What (a)biotic factors influence supply/demand of resources and affect trade patterns? | Manipulate conditions to increase/decrease value of a resource; track effects on trade |
| Hoarding | Do microbes hoard resources? | Track resource storage, particularly in "farmers" |
| | Do microbes trade hoarded resources at a later stage? | Manipulate market conditions so trade is not beneficial; change supply/demand to see trade increase. |

species preferentially supporting rhizobial symbionts that provide more fixed $N_2$ for hosts (39–41) and in the arbuscular mycorrhizal mutualism in which host plants allocate more carbon resources to fungal strains providing more nutrient resources (42, 43).

However, can microbes also discriminate among their hosts? In the mycorrhizal mutualism, an individual fungus (i.e., a single multicellular genotype) can potentially compare resource allocation of several hosts simultaneously because it is connected underground to multiple plants (44, 45). Research suggests that mycorrhizal fungi can evaluate the quality of these hosts and adjust resource allocation patterns accordingly, allowing for market dynamics to emerge (43, 46, 47). It remains an open question how this information is integrated over the fungal network and over what distances this evaluation can take place.

Discrimination, which involves choosiness and searching, is generally associated with costs (27). This implies that for discrimination ability to evolve there must be (*i*) sufficient variation in trader quality and (*ii*) a fitness benefit for partnering with higher-quality individuals. Additionally, if discrimination occurs before actual investment in the interaction, the potential problem faced by a discriminating trading partner is that of "false advertising" (i.e., if a candidate partner honestly reflects its value as partner) (48, 49). Recent research addresses how fungi sense differences in quality (50) and has used phenotypic plasticity models to ask how trading strategies are influenced by fluctua-

tions in market conditions such as external nutrient availability (51).

**Strategy Two: Build Local Business Ties.** In a market, your local environment determines your trade connections. Simultaneous comparisons are not always possible to identify the best partners. Nonfilamentous organisms, such as most bacteria, have fewer opportunities than filamentous microbes like mycorrhizal fungi to interact simultaneously with multiple partners. If direct discrimination among trading partners is more difficult, can market conditions still arise?

Theoretical work suggests that spatial structuring of partners can limit the spread of less beneficial partners and favor the evolution of cooperative exchanges (52, 53). This is because spatial structure offers a way to keep benefits close to cooperators, rather than diffusing to others. Similarly, spatial structure can also potentially promote the origin and maintenance of microbial markets. Market theory predicts that the success and stability of markets will depend on the extent to which cooperators gain more access to resources than noncooperators (3). Spatial structure facilitates the creation of physical connections to profitable partners, limits diffusion of costly substances, and reduces the number of potential partners to evaluate compared with well-mixed environments. As a result, spatial structure could increase the effectiveness of partner discrimination, particularly for nonfilamentous microbes, where such discrimination is otherwise more difficult. Consequently, a major question is whether

the stability of microbial markets depends on spatially structured environments (54).

An illustration of the importance of spatial structure for a potential microbial market was found in a recent experiment in which cooperation was evolved de novo in cocultures of two bacterial species (*Salmonella enterica* ser. Typhimurium and *Escherichia coli*) (55). In this system, *Salmonella* facilitated the growth of its partner by secreting a costly amino acid, whereas *E. coli* reciprocated through processing accumulating waste. Preferential reciprocation of cooperative genotypes was found to only occur in a spatially structured (solid) environment, leading to increased densities of both species within 10 generations. In contrast, in unstructured environments (liquid media), cooperation did not evolve. This illustrates how novel synthetic markets can arise, given the appropriate selective conditions.

If being spatially aggregated is individually beneficial, physical structures may evolve in which trade is conducted and maintained. In a mutualism between sulfur-reducing, chemotrophic bacteria and phototrophic sulphide oxidizers, spatially organized aggregates called consortia are formed (56, 57), potentially allowing for more controlled resource flow (56, 58). Likewise, cross-feeding mutualisms between hydrogen-producing fermenters and methanogens (e.g., in sewage sludge) form aggregative flocs to retain shared metabolites (54). Consortia and flocs are common in microbial communities (58, 59). Such aggregations may even represent the starting point for mutualisms in which one organism

eventually compartmentalizes the other in a specific structure.

However, the effect of structure on microbial exchange is not straightforward (60); benefits of increased spatial structure can sometimes be negated by the negative effects of competition among relatives (61, 62). A second problem is that markets can be parasitized by third parties that use metabolites without contributing to the exchange (63). In biological markets, traders are predicted to evolve mechanisms to avoid losses to nontrading partners. This is particularly important in resource-poor environments (64). Parasitism can potentially be limited if microbes are able to create direct (physical) connections to trade resources. Metal-reducing bacteria like *Geobacter sulfurreducens* form pili that function as microbial nanowires (65). These wires probably allow the transfer of electrons to other *Geobacter* species over manifolds the size of bacteria (66, 67). Although very little is known about these transfers, this is intriguing because it suggests a potential mechanism to direct resources (e.g., electrons) to specific microbial partners. Other forms of (temporary) adhesion between partners may likewise direct resource transfer to high-quality trading partners. More research is needed to understand how the potential for directed transfers depends on the microbial environment, for example, the presence of dense microbial biofilms vs. simple well-mixed environments.

**Strategy Three: Diversify or Specialize.** In market terms, diversification in commodities (i.e., offering multiple services or goods rather than only a single one) is a strategy that could reduce exposure to price volatility. In theory, diversification reduces risks associated with volatile market conditions, thereby facilitating more consistent performance under a wider range of conditions. In contrast, through commodity specialization, a trader can usually offer a good at a lower price, increasing its chances to outbid competitors (Box 1, condition iv) (11, 22, 23).

In microbial markets, the individual advantages of using diversified or specialized strategies will depend strongly on context (11, 37). Diversification of services or commodities can be favored if this strategy increases the range of environmental conditions over which a trader remains a useful partner. For instance, the actinobacterial symbionts of leaf-cutter ants produce antibiotics that inhibit *Escovopsis*, a parasitic fungus invading fungal gardens (68). Recent work suggests these symbionts provide a more diversified service by also providing ant

workers themselves with broad spectrum protection against infectious fungi, including entomopathogenic (e.g., *Metarhizium anisopliae*) infections (69). This dual service can increase ant incentives to maintain bacterial communities even in the absence of specific parasitic threats or direct immune challenges.

In contrast, specialized trade occurs when a trading partner provides only a single service or good and is predicted to be favored when there is strong competition within a trader class (i.e., when many competing traders are offering the same commodity). This is because organisms often experience tradeoffs in the acquisition of various resources (22, 23). If there is such a tradeoff, a specialized microbe offering only one resource would be able to offer a better price for that resource than a microbe offering multiple resources. In human economics, this "law of comparative advantage" was first proposed two centuries ago by David Ricardo, arguing that it is beneficial to specialize in the acquisition of one commodity and obtain the other through trade (70). In a recently discovered exchange between a nitrogen-fixing unicellular cyanobacterium and a tiny single-celled prymnesiophytes algal partner (71), the cyanobacterium has lost its ability to carry out its own photosynthesis and receives carbon from this specific algal partner in exchange for fixed N. It is unknown whether there is a tradeoff between N fixation and photosynthesis in this cyanobacterium. However, this case raises the intriguing question of whether through the loss of photosynthesis, this cyanobacterium can fix N more efficiently and consequently offer a better price than other symbiotic cyanobacteria or generalist planktonic species competing for algal carbon.

How can market theory generate hypotheses on the evolution of specialized vs. diversified services in microbial markets? One idea is that high dependence on a partner promotes diversification. By studying or even synthetically creating microbial trade markets (e.g., ref. 72) with partners displaying different levels of dependency and competition, we may be able to test empirically when the benefits of diversification outweigh those of specialization. A second question is whether diverse services arise as byproducts or whether microbial partners are under selection to vary benefits to hosts? The costs of providing diverse benefits will be affected by tradeoffs associated with their provisioning. Diversification is predicted to emerge if commodities provided by one partner are positively correlated, whereas specialization would be favored by a tradeoff in the acquisition of two commodities (22, 23).

**Strategy Four: Become Indispensable.** In economics, if a partner is indispensable, the price it receives is predicted to be high. This is because by restricting choice an economic actor can monopolize market exchange (14, 73). From a biological market perspective, monopolistic control of vital partner functions, such as reproduction, by microbial mutualists increases their market value. Partners are less likely or able to discontinue trade because this could result in negative fitness consequences and even death. Although indispensability cannot always be considered indicative of an active strategy used by microbes to command higher prices (i.e., it can result from a coevolutionary process involving both host and microbe or two microbes), the end result is a monopolistic position. As in economic markets, microbial partners still face risks of being undercut by another microbe offering a better price. Therefore, the best examples of microbes using this strategy involve tight physical ties, for example, those associated with endosymbiosis (e.g., refs. 74 and 75), which limit the potential for partner switching. If it is difficult or impossible to switch to another microbe from the environment, the prevailing partner would occupy a monopolistic position and be indispensable.

In some cases, hosts have relied on microbial mutualisms to such an extent that this dependency has driven an evolutionary loss of host traits (76). For example, several genes involved in amino acid biosynthesis have been lost in the pea aphid *Acyrthosiphon pisum*. These are encoded in the genome of *Buchnera*, the aphid's symbiont (77). Corals (*Acropora* sp.) have lost the ability to synthesize cysteine, because this is provided by their endosymbionts (78). Hundreds of marine worm species show loss of traits for digestive or excretory systems because of their evolved dependence on chemosynthetic microbes for digestion (79). The microbes benefit from protection and are provided with a suitable habitat, whereas the host is able to survive on inorganic energy and carbon sources, allowing them to flourish in harsh conditions (80). As a result of vital trait loss, these microbial symbionts become fully indispensable to their hosts. An important research question, although empirically challenging, is to test whether indispensable microbial partners command higher prices compared with symbioses where the host is not fully dependent on its microbial partners. This effect would only be predicted to occur in cases where the potential for switching to another microbial partner is limited. Without such limitations, indispensability of individual microbes driving up prices could be

counteracted by outbidding competition by microbes from the environment.

**Strategy Five: Save for a Rainy Day.** Careful management of resources is important for traders engaged in market exchange. This can mean saving resources for future trade, rather than consuming or trading immediately. Humans and some other animals practice such management in agriculture or food storage where a portion of material is maintained rather than consumed (81, 82), so it can be propagated for subsequent generations, or sold later at a better price. We expect such hoarding of market resources for future trade if three conditions apply: (*i*) the supply of the resource is volatile to such an extent that there are periods of luxury supply (i.e., the trader can afford not to use it all); (*ii*) there is volatility in demand from the other trader class; and (*iii*) it is storable.

Microbes can also practice prudent management of resources and even increase their capital, like some animals. For example, there is evidence that rather than providing hosts with phosphorus, some mycorrhizal fungal strains can store the phosphorus nutrients they have collected or keep them in a form inaccessible to hosts (43, 83). Such speculation with resources potentially allows a fungal partner to gain a better carbon price for their nutrients, as soil nutrient levels become depleted.

The social amoeba *Dictyostelium discoideum* has been shown to farm bacteria before consuming them. For most of their life cycle, *D. discoideum* consume bacteria via phagocytosis and divide by binary fission, but under starvation conditions, they aggregate into a multicellular slug that differentiates to contain a sterile stalk, as well as hardy spores (84). About one-third of *D. discoideum* clones carry bacteria through the normally sterile spore stage and then release the bacteria to propagate them in an environment where they proliferate. Once the bacteria reach sufficient densities in the favorable habitat, the amoeba farmers consume the bacterial crop (85). Farming strains devoured fewer than half the bacteria present, whereas nonfarmers consumed nearly all of the bacteria (85). This illustrates that microbes (whether or not they are active traders) are able to prudently save resources for future use, which may be important for microbial markets to evolve. This strategy is most likely to evolve in microbial markets consisting of a larger partner using a smaller one (e.g., amoeba–bacteria interactions). More generally, farming strategies are likely to evolve when there is a larger partner that is dependent on harvesting or milking a

smaller one (e.g., refs. 82 and 86). Future work should determine whether volatility in market demand or in resource abundance are indeed factors promoting hoarding of resources for future trade.

**Strategy Six: Eliminate the Competition.** Although direct elimination of competition is a deviation from biological market assumptions, antagonism against other individuals in one's trader class can help secure favorable trade conditions for the individual using them (2, 3). For example, monopolistic control of chacma baboon mating markets through competitor suppression by alpha males has been observed (14). When costs of directly suppressing competitors are small or competition is intense, these types of antagonistic strategies are likely to be favored over outbidding competition. Coercion rather than leverage becomes the dominant force driving trade. However, if competitors are completely eliminated, market dynamics will disappear because the only trader left becomes a monopolist.

To eliminate competitors directly and secure greater market control, microbes could use a variety of strategies, including bacteriocin production (52, 87, 88). Bacteriocins are a class of toxins produced by bacteria to inhibit competing strains. Microbes produce bacteriocins that typically target closely related rather than distantly related strains within the same species, because these are most likely to compete for similar resources (89, 90). In this way, competing strains can be eliminated, and the bacteriocin producer can achieve a resource monopoly. To avoid targeting related clones, kin-recognition systems, like toxin–antidote systems, are often used (91). For example, *E. coli* deploys toxins to eliminate competing strains, while using immunity genes specific to these toxins to protect itself (92).

In leaf-cutter fungal gardens, resident basidiomycete fungi produce incompatibility compounds that effectively kill intruding fungal strains, and this antagonistic interaction increases with increasing genetic distance (93). Worker ants also help distribute toxins that prevent alien fungi from establishing. This is possible because antagonistic compounds of fungal origin are ingested by ants when feeding on the resident fungus and become part of the fecal droplets that ants use to fertilize fungus gardens (94). Application of such droplets to alien tissue generally eliminates alien fungi (93). By eliminating competing alien strains, the resident fungus thus is able to monopolize the ant host leaf supply, securing a greater share of the resources provided to the fungal gardens.

The mutualism between insect-killing *Xenorhabdus* bacterial symbionts and entomopathogenic *Steinernema* nematodes is a potentially useful system to study competition in a market framework (95–97). *Xenorhabdus bovienii* use toxins to kill insects in which the nematode reproduces. When nematodes migrate to find new insect prey, they take only a few clones of *X. bovienii* (97), and thus competition for migrating nematode hosts is intense. *X. bovienii* clones use bacteriocins to ensure access to migrating host resources (95–97). Initial work on field populations suggests that, in line with predictions (e.g., ref. 89), bacteriocins most strongly mediate intraspecific competition but that they also play a role in mediating coexisting species (97). Because of intense within-trader class competition in this system, competition is expected to be strong and antagonistic strategies to control market access are likely to evolve.

## Discussion and Perspectives

Although research on microbial social interactions has greatly expanded in recent years, there has been a limited attempt to study microbial exchange systems using a market framework. Studies on microbial markets have either been purely theoretical (11, 22, 23, 36, 37), whereas more empirical work has only tested these ideas in plant root mutualisms (40, 42, 43, 49, 98). We argue that biological market theory can help structure how we interpret and explain the wide range of collaborative behaviors performed by microbes, generating new hypotheses and approaches in social microbiology. At the same time, we recognize that it is still unknown whether a substantial number of microbial mutualisms fully conform to the conditions for biological markets (Box 1). Consequently, it will remain difficult to assess the importance of microbial markets before more research explicitly evaluating trade in microbes is performed. Below we address some specific questions that help answer this question.

Regardless of the actual importance in natural conditions, microbial systems are incredibly amenable to study markets: (*i*) resources can be easily manipulated; (*ii*) resource exchange can be quantitatively tracked; (*iii*) and short generation times mean that market changes can be studied on an evolutionary time scale (experimental evolution). These advantages also mean that microbial systems can potentially be used to test longstanding questions in biological market theory, including how prices are set in nature, how environmental variation

influences trade strategies, or the importance of false vs. honest advertising. Another valuable contribution will be to study microbial markets and compare them to animal markets (Box 1). This could help us to determine which, if any, market features are specific to cognitive agents (34, 35). Experimental evolution approaches can be particularly useful for studying microbial markets because they can circumvent the difficulties in inferring adaptations from behaviors exhibited by naturally evolved microbes. Below, we propose some questions that warrant particular attention and may be successfully approached using a microbial market framework (Table 1).

**Evolution of Variation in Partner Quality.** An important assumption of biological market theory is that there is sufficient individual variation in partner quality to make choosiness worthwhile. Hence, a key step to understanding the evolution of microbial markets is the notion of individual variation in partner quality. Advances in the study of microbial individuality have revealed that the typical population-level focus in microbiology can mask the existence of different phenotypes in microbial communities (99, 100). Individuality (i.e., cell-to-cell phenotypic variability) of bacteria is an important factor driving microbial ecology and evolution (101, 102). Future research should aim to study this phenotypic variation between microbial individuals, particularly in terms of trading partner quality. The study of such variation, particularly the identification of beneficial strains, is also of practical application for mutualistic systems (e.g., rhizobial and mycorrhizal mutualisms) that can be better optimized for human benefit (103).

**How Does Partner Discrimination Evolve?** A key element of any market is that discrimination among partners is based on the benefit they provide. In mycorrhizal mutualisms, there is a potential for this to evolve because individuals are able to simultaneously monitor and compare resource flows to and from different trading partners in a single trading network (43, 46). In free-living microbes, there is less potential for such simultaneous comparisons. However, microbes can exert control over their location through chemotaxis (104). If free-living microbes migrate to locations closer to high-quality trading partners and then locally release their commodity, this can facilitate the evolution of partner choice. For example, chemotactic choice could play a role in cases where rhizosphere microbes migrate toward host root exudates (105, 106), providing the most attractive host with the highest number of microbial partners to choose from. Such chemotactic partner choice is probably more difficult to achieve in dense polymicrobial biofilms than in less dense liquid environments with clear concentration gradients. To test market-based partner discrimination in chemotactic mutualisms, choice experiments could test whether individuals move toward high-quality trading partners. Experiments could run for several generations to see whether greater discrimination and migration begin to evolve and under which conditions (for instance, in biofilms vs. free-living conditions or in filamentous, multicellular microbes vs. in single-celled microbes).

If partner discrimination becomes so effective that only high-quality genotypes can survive, variations in partner quality could ultimately be lost (107, 108). In these fixed populations, there is no longer variability in prices, theoretically ending market dynamics. However, in natural systems, which are constantly exposed to environmental volatility, the best-quality genotype can vary depending on market conditions. Such context dependence could cause variation in preferential allocation of resources to trading partners, potentially counteracting this loss in diversity.

In contrast, there might be microbial trading interactions where the microbial partner cannot achieve partner choice. This could, for instance, be the case in endosymbionts that have no (or only limited) active horizontal transmission. In these cases, the microbial market would reduce to a host-controlled monopoly (e.g., ref. 14). Partner choice models might still be useful in these circumstances because variation in host demand for particular microbial commodities may be influenced by environmental conditions, and this could be analyzed with market theory.

**How Do Markets Evolve Under Fluctuations in Supply and Demand?** One market prediction that could be tested in microbial systems is that the benefit of trade depends not only on the interacting partners but also on the available supply of commodities from other sources. Analogous to primate markets, where the number of infants and fertile females influences the value they represent (109, 110), microbial experiments are possible in which the abundance of a resource is externally manipulated to change the balance of trade costs and benefits. We predict that biotic or abiotic conditions that influence the demand for a particular service [e.g., a rise in temperature if the service is heat resistance (111)] will influence its value on the microbial market: when demand is higher, a higher price can be asked for that service. Microbial systems are useful to study the intricacies of this problem. This is of particular relevance for supply and demand variations induced by climate change and the response of mutualisms to these changes (112). Another example is in agriculture: the application of fertilizer can reduce the market value of microbial mutualists providing nutrients to plant host and thus drive a reduction in their reliance on mutualistic microbial partners (113, 114).

**The Evolution of Microbial Markets from Noncooperative Interactions.** Evolutionary biologists are interested in understanding the transitions that drive facultative exchanges into obligate ones. Microbial markets offer a unique opportunity to reenact major transitions using experimental evolution approaches. For example, the recently introduced Black Queen Hypothesis (115, 116) suggests that the inherent leakiness of many microbial public goods results in microbes being selected to lose the ability to produce certain goods themselves, as long as these goods are provided by helper microbes in the community. This dependence is predicted to drive the evolution of cooperative phenotypes in which the beneficiary benefits the helper, sustaining its population (115). In this way, obligate microbial cooperative interactions, and potentially rudimentary microbial markets, can evolve from previously noncooperative interactions. Experimental evolution approaches (e.g., ref. 117), can be useful to understand the loss of traits in microbial communities and what selection pressures favor an increased dependence on Black Queen markets.

**Hoarding and Microbial Prudence.** Prudence is often associated with advanced cognitive capacities, but it is not a requirement if direct physiological responses to varying resource levels are used to achieve real-time collaboration (35). In the legume–rhizobia mutualism, some rhizobial strains use a chemical called rhizobitoxine that can substantially increase the accumulation of carbon [as poly-3-hydroxybutyrate (PHB)] while reducing the growth of the legume host and competing rhizobial strains. This helps increase rhizobial reproduction and long-term survival under starvation conditions (118, 119). Recent work suggests that the manner in which PHB resources are hoarded is conditional, with a rhizobial strain producing fewer high-PHB cells when low competitor density predicts only short-term starvation (118) and can thus be understood

as a hoarding strategy in response to competition. This system, and others like *Dictyostelium* farming (85) and the ectomycorrhizal soil fungus *Morchella crassipes* farming *Pseudomonas putida* bacteria as a carbon source (86), can be used to study under what conditions scarce resources are held, so they can be either used later or traded for a greater profit in the future.

**Applied Microbial Markets.** Lastly, there is potential applied value in using biological market theory to help identify the conditions under which trade is maximized for particular partners. This could have benefits in agriculture and medicine. In agriculture, natural selection favors microbes that maximize their own fitness and gain of resources over that of their host or competitors. This can conflict with the goals of agriculture or other industries, where humans favor microbes that maximize yields of their crop hosts or other products (120). Once we have a better understanding of the conditions under which microbes transfer more resources, we can use experimental manipulations to select for microbes offering better market prices to their hosts (103). Likewise in medicine, an increased understanding of trade by pathogenic microbes might be useful to disrupt these markets and promote host health. Recent work suggests that host partner choice is important in shaping gut microbiota composition (121), which has a key role in shaping human and animal health and behavior (122, 123). Do hosts use market principles to guide their selection of microbial partners and optimize their gut microbiota?

## Conclusion

Biological market theory offers a potentially valuable framework for studying microbial cooperation among species. We predict that its primary contribution will be to generate new experimental questions and hypotheses in the field of social microbiology. Also, applying market theory to microbial mutualisms will be an important test of the robustness of market-based principles as a more general principle of social behavior. We identified six strategies microbes use or benefit from to optimize their success in markets. This list will no doubt grow as researchers uncover new ways in which microbes manipulate trade in their favor. Because they are typically easy to manipulate, microbial markets will be useful systems for testing questions about biological markets in general (Table 1). These include the evolution of partner choice, responses to price fluctuations,

and identification of the market conditions that drive specialization vs. diversification, while simultaneously taking into account the biological context of exchange. In the current era of synthetic biology, a microbial market perspective can increase our understanding of the complex feedbacks among partners and inspire the engineering of novel interactions. This will both drive forward our understanding of microbiology and increase our knowledge of cooperation in general.

1 Burt RS (2004) Structural holes and good ideas. *Am J Sociol* 110(2):349–399.
2 Noë R, Hammerstein P (1994) Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol* 35(1):1–11.
3 Noë R, Hammerstein P (1995) Biological markets. *Trends Ecol Evol* 10(8):336–339.
4 Edwards DP, Hassall M, Sutherland WJ, Yu DW (2006) Selection for protection in an ant-plant mutualism: Host sanctions, host modularity, and the principal-agent game. *Proc Biol Sci* 273(1586):595–602.
5 Johnstone RA, Bshary R (2008) Mutualism, market effects and partner control. *J Evol Biol* 21(3):879–888.
6 Bronstein JL (1994) Our current understanding of mutualism. *Q Rev Biol* 69(1):31–51.
7 McFall-Ngai M, et al. (2013) Animals in a bacterial world, a new imperative for the life sciences. *Proc Natl Acad Sci USA* 110(9):3229–3236.
8 Berendsen RL, Pieterse CMJ, Bakker PAHM (2012) The rhizosphere microbiome and plant health. *Trends Plant Sci* 17(8):478–486.
9 Desbrosses GJ, Stougaard J (2011) Root nodulation: A paradigm for how plant-microbe symbiosis influences host developmental pathways. *Cell Host Microbe* 10(4):348–358.
10 West SA, Diggle SP, Buckling A, Gardner A, Griffin AS (2007) The social lives of microbes. *Annu Rev Ecol Evol Syst* 38:53–77.
11 Kummel M, Salant SW (2006) The economics of mutualisms: Optimal utilization of mycorrhizal mutualistic partners by plants. *Ecology* 87(4):892–902.
12 Xia D, et al. (2012) Grooming reciprocity in female tibetan macaques macaca thibetana. *Am J Primatol* 74(6):569–579.
13 Gumert MD (2007) Payment for sex in a macaque mating market. *Anim Behav* 74(6):1655–1667.
14 Clarke PMR, Halliday JEB, Barrett L, Henzi SP (2010) Chacma baboon mating markets: Competitor suppression mediates the potential for intersexual exchange. *Behav Ecol* 21(6):1211–1220.
15 Völkl W, Woodring J, Fischer MK, Lorenz MW, Hoffmann KH (1999) Ant-aphid mutualisms: The impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia* 118(4):483–491.
16 Stadler B, Dixon AFG (2005) Ecology and evolution of aphid-ant interactions. *Annu Rev Ecol Evol Syst* 36:345–372.
17 Port M, Clough D, Kappeler PM (2009) Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs, Eulemur fulvus rufus. *Anim Behav* 77(1):29–36.
18 Fruteau C, Lemoine S, Hellard E, van Damme E, Noë R (2011) When females trade grooming for grooming: Testing partner control and partner choice models of cooperation in two primate species. *Anim Behav* 81(6):1223–1230.
19 Kutsukake N, Clutton-Brock TH (2010) Grooming and the value of social relationships in cooperatively breeding meerkats. *Anim Behav* 79(2):271–279.
20 Bshary R, Grutter AS (2002) Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: The cleaner fish case. *Ecol Lett* 5(1):130–136.
21 Akçay E, Simms EL (2011) Negotiation, sanctions, and context dependency in the legume-Rhizobium mutualism. *Am Nat* 178(1):1–14.
22 Schwartz MW, Hoeksema JD (1998) Specialization and resource trade: Biological markets as a model of mutualisms. *Ecology* 79(3):1029–1038.
23 Hoeksema JD, Schwartz MW (2003) Expanding comparative-advantage biological market models: Contingency of mutualism on partners' resource requirements and acquisition trade-offs. *Proc Biol Sci* 270(1518):913–919.
24 Leimar O, Hammerstein P (2010) Cooperation for direct fitness benefits. *Philos Trans R Soc Lond B Biol Sci* 365(1553):2619–2626.
25 Fischer MEK, Völkl WO, Hoffmann KLH (2005) Honeydew production and honeydew sugar composition of polyphagous black bean aphid, Aphis fabae (Hemiptera: Aphididae) on various host plants and implications for ant-attendance. *Eur J Entomol* 102(2):155–160.
26 Norscia I, Antonacci D, Palagi E (2009) Mating first, mating more: Biological market fluctuation in a wild prosimian. *PLoS ONE* 4(3):e4679.
27 McNamara JM, Leimar O (2010) Variation and the response to variation as a basis for successful cooperation. *Philos Trans R Soc Lond B Biol Sci* 365(1553):2627–2633.
28 Nowak MA (2006) Five rules for the evolution of cooperation. *Science* 314(5805):1560–1563.
29 Adam TC (2010) Competition encourages cooperation: Client fish receive higher-quality service when cleaner fish compete. *Anim Behav* 79(6):1183–1189.
30 Bshary R, Schäffer D (2002) Choosy reef fish select cleaner fish that provide high-quality service. *Anim Behav* 63(3):557–564.
31 Fruteau C, Voelkl B, van Damme E, Noë R (2009) Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc Natl Acad Sci USA* 106(29):12007–12012.
32 Suchak M, de Waal FBM (2012) Monkeys benefit from reciprocity without the cognitive burden. *Proc Natl Acad Sci USA* 109(38):15191–15196.
33 Cheney DL (2011) Extent and limits of cooperation in animals. *Proc Natl Acad Sci USA* 108(Suppl 2):10902–10909.
34 Noë R (2006) Cooperation experiments: Coordination through communication versus acting apart together. *Anim Behav* 71(1):1–18.
35 Brosnan SF, Salwiczek L, Bshary R (2010) The interplay of cognition and cooperation. *Philos Trans R Soc Lond B Biol Sci* 365(1553):2699–2710.
36 Cowden CC, Peterson CJ (2009) A multi-mutualist simulation: Applying biological market models to diverse mycorrhizal communities. *Ecol Modell* 220(12):1522–1533.
37 Grman E, Robinson TMP, Klausmeier CA (2012) Ecological specialization and trade affect the outcome of negotiations in mutualism. *Am Nat* 179(5):567–581.
38 Gore J, Youk H, van Oudenaarden A (2009) Snowdrift game dynamics and facultative cheating in yeast. *Nature* 459(7244):253–256.
39 Kiers ET, Rousseau RA, West SA, Denison RF (2003) Host sanctions and the legume-rhizobium mutualism. *Nature* 425(6953):78–81.
40 Simms EL, et al. (2006) An empirical test of partner choice mechanisms in a wild legume-rhizobium interaction. *Proc Biol Sci* 273(1582):77–81.
41 Oono R, Anderson CG, Denison RF (2011) Failure to fix nitrogen by non-reproductive symbiotic rhizobia triggers host sanctions that reduce fitness of their reproductive clonemates. *Proc Biol Sci* 278(1718):2698–2703.
42 Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M (2009) Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecol Lett* 12(1):13–21.
43 Kiers ET, et al. (2011) Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science* 333(6044):880–882.
44 Giovannetti M, Sbrana C, Avio L, Strani P (2004) Patterns of below-ground plant interconnections established by means of arbuscular mycorrhizal networks. *New Phytol* 164(1):175–181.
45 Mikkelsen BL, Rosendahl S, Jakobsen I (2008) Underground resource allocation between individual networks of mycorrhizal fungi. *New Phytol* 180(4):890–898.
46 Lekberg Y, Hammer EC, Olsson PA (2010) Plants as resource islands and storage units—adopting the mycocentric view of arbuscular mycorrhizal networks. *FEMS Microbiol Ecol* 74(2):336–345.
47 Selosse M-A, Rousset F (2011) Evolution. The plant-fungal marketplace. *Science* 333(6044):828–829.

**48** Fraser B (2013) *Cooperation and Its Evolution*, eds Sterelny K, Joyce R, Calcott B, Fraser B (MIT Press, Cambridge, MA), pp 153–174.

**49** Gubry-Rangin C, Garcia M, Béna G (2010) Partner choice in Medicago truncatula-Sinorhizobium symbiosis. *Proc Biol Sci* 277(1690):1947–1951.

**50** Fellbaum CR, et al. (2012) Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. *Proc Natl Acad Sci USA* 109(7):2666–2671.

**51** Behm JE, Kiers ET A phenotypic plasticity framework for assessing intraspecific variation in arbuscular mycorrhizal fungal traits. *J Ecol*, in press.

**52** Frank SA (1994) Spatial polymorphism of bacteriocins and other allelopathic traits. *Evol Ecol* 8(4):369–386.

**53** Lion S, Baalen Mv (2008) Self-structuring in spatial evolutionary ecology. *Ecol Lett* 11(3):277–295.

**54** Wintermute EH, Silver PA (2010) Dynamics in the mixed microbial concourse. *Genes Dev* 24(23):2603–2614.

**55** Harcombe W (2010) Novel cooperation experimentally evolved between species. *Evolution* 64(7):2166–2172.

**56** Overmann J, Schubert K (2002) Phototrophic consortia: Model systems for symbiotic interrelations between prokaryotes. *Arch Microbiol* 177(3):201–208.

**57** Müller J, Overmann J (2011) Close interspecies interactions between prokaryotes from sulfureous environments. *Front Microbiol* 2:146.

**58** Overmann J (2004) *Symbiosis Mechanisms and Model Systems*, ed Sekbach J (Kluwer, Dordrecht, The Netherlands), pp 241–255.

**59** Boetius A, et al. (2000) A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature* 407(6804):623–626.

**60** Verbruggen E, et al. (2012) Spatial structure and interspecific cooperation: Theory and an empirical test using the mycorrhizal mutualism. *Am Nat* 179(5):E133–E146.

**61** Taylor PD (1992) Altruism in viscous populations - an inclusive fitness model. *Evol Ecol* 6(4):352–356.

**62** Wilson D, Pollock G, Dugatkin L (1992) Can altruism evolve in purely viscous populations? *Evol Ecol* 6(4):331–341.

**63** Boyle RA, Williams HTP, Lenton TM (2012) Natural selection for costly nutrient recycling in simulated microbial metacommunities. *J Theor Biol* 312C:1–12.

**64** Nakajima T, Sano A, Matsuoka H (2009) Auto-/heterotrophic endosymbiosis evolves in a mature stage of ecosystem development in a microcosm composed of an alga, a bacterium and a ciliate. *Biosystems* 96(2):127–135.

**65** Reguera G, et al. (2005) Extracellular electron transfer via microbial nanowires. *Nature* 435(7045):1098–1101.

**66** Summers ZM, et al. (2010) Direct exchange of electrons within aggregates of an evolved syntrophic coculture of anaerobic bacteria. *Science* 330(6009):1413–1415.

**67** Morita M, et al. (2011) Potential for direct interspecies electron transfer in methanogenic wastewater digester aggregates. *MBio* 2(4):e00159–e11.

**68** Little AEF, Murakami T, Mueller UG, Currie CR (2006) Defending against parasites: Fungus-growing ants combine specialized behaviours and microbial symbionts to protect their fungus gardens. *Biol Lett* 2(1):12–16.

**69** Mattoso TC, Moreira DDO, Samuels RI (2012) Symbiotic bacteria on the cuticle of the leaf-cutting ant Acromyrmex subterraneus subterraneus protect workers from attack by entomopathogenic fungi. *Biol Lett* 8(3):461–464.

**70** Ricardo D (1817) *On the Principles of Political Economy and Taxation* (John Murray, London, UK).

**71** Thompson AW, et al. (2012) Unicellular cyanobacterium symbiotic with a single-celled eukaryotic alga. *Science* 337(6101):1546–1550.

**72** Kim HJ, Boedicker JQ, Choi JW, Ismagilov RF (2008) Defined spatial structure stabilizes a synthetic multispecies bacterial community. *Proc Natl Acad Sci USA* 105(47):18188–18193.

**73** Hammerstein P, Hagen EH (2005) The second wave of evolutionary economics in biology. *Trends Ecol Evol* 20(11):604–609.

**74** Partida-Martinez LP, Monajembashi S, Greulich K-O, Hertweck C (2007) Endosymbiont-dependent host reproduction maintains bacterial-fungal mutualism. *Curr Biol* 17(9):773–777.

**75** Lackner G, Moebius N, Partida-Martinez LP, Boland S, Hertweck C (2011) Evolution of an endofungal lifestyle: Deductions from the Burkholderia rhizoxinica genome. *BMC Genomics* 12:210.

**76** Ellers J, Kiers ET, Currie CR, McDonald BR, Visser B (2012) Ecological interactions drive evolutionary loss of traits. *Ecol Lett* 15(10):1071–1082.

**77** Richards S, et al.; International Aphid Genomics Consortium (2010) Genome sequence of the pea aphid Acyrthosiphon pisum. *PLoS Biol* 8(2):e1000313.

**78** Shinzato C, et al. (2011) Using the Acropora digitifera genome to understand coral responses to environmental change. *Nature* 476(7360):320–323.

**79** Dubilier N, Bergin C, Lott C (2008) Symbiotic diversity in marine animals: The art of harnessing chemosynthesis. *Nat Rev Microbiol* 6(10):725–740.

**80** Kleiner M, et al. (2012) Metaproteomics of a gutless marine worm and its symbiotic microbial community reveal unusual pathways for carbon and energy use. *Proc Natl Acad Sci USA* 109(19):E1173–E1182.

**81** Brodin A (2005) Mechanisms of cache retrieval in long-term hoarding birds. *J Ethol* 23(2):77–83.

**82** Ivens AB, Kronauer DJ, Pen I, Weissing FJ, Boomsma JJ (2012) Ants farm subterranean aphids mostly in single clone groups—an example of prudent husbandry for carbohydrates and proteins? *BMC Evol Biol* 12:106.

**83** Hammer EC, Pallon J, Wallander H, Olsson PA (2011) Tit for tat? A mycorrhizal fungus accumulates phosphorus under low plant carbon availability. *FEMS Microbiol Ecol* 76(2):236–244.

**84** Kessin RH (2001) *Dictyostelium: Evolution, Cell Biology, and the Development of Multicellularity* (Cambridge Univ Press, Cambridge, UK).

**85** Brock DA, Douglas TE, Queller DC, Strassmann JE (2011) Primitive agriculture in a social amoeba. *Nature* 469(7330):393–396.

**86** Pion M, et al. (2013) Bacterial farming by the fungus Morchella crassipes. *Proc Biol Sci* 280(1773):20132242.

**87** Chao L, Levin BR (1981) Structured habitats and the evolution of anticompetitor toxins in bacteria. *Proc Natl Acad Sci USA* 78(10):6324–6328.

**88** Riley MA (1998) Molecular mechanisms of bacteriocin evolution. *Annu Rev Genet* 32:255–278.

**89** Gardner A, West SA, Buckling A (2004) Bacteriocins, spite and virulence. *Proc Biol Sci* 271(1547):1529–1535.

**90** Schoustra SE, Dench J, Dali R, Aaron SD, Kassen R (2012) Antagonistic interactions peak at intermediate genetic distance in clinical and laboratory strains of Pseudomonas aeruginosa. *BMC Microbiol* 12:40.

**91** Strassmann JE, Gilbert OM, Queller DC (2011) Kin discrimination and cooperation in microbes. *Annu Rev Microbiol* 65:349–367.

**92** Cascales E, et al. (2007) Colicin biology. *Microbiol Mol Biol Rev* 71(1):158–229.

**93** Poulsen M, Boomsma JJ (2005) Mutualistic fungi control crop diversity in fungus-growing ants. *Science* 307(5710):741–744.

**94** Schiøtt M, Rogowska-Wrzesinska A, Roepstorff P, Boomsma JJ (2010) Leaf-cutting ant fungi produce cell wall degrading pectinase complexes reminiscent of phytopathogenic fungi. *BMC Biol* 8:156.

**95** Hawlena H, Bashey F, Lively CM (2010) The evolution of spite: Population structure and bacteriocin-mediated antagonism in two natural populations of xenorhabdus bacteria. *Evolution* 64(11):3198–3204.

**96** Hawlena H, Bashey F, Mendes-Soares H, Lively CM (2010) Spiteful interactions in a natural population of the bacterium Xenorhabdus bovienii. *Am Nat* 175(3):374–381.

**97** Bashey F, Young SK, Hawlena H, Lively CM (2012) Spiteful interactions between sympatric natural isolates of Xenorhabdus bovienii benefit kin and reduce virulence. *J Evol Biol* 25(3):431–437.

**98** Simms EL, Taylor DL (2002) Partner choice in nitrogen-fixation mutualisms of legumes and rhizobia. *Integr Comp Biol* 42(2):369–380.

**99** Amantonico A, Urban PL, Fagerer SR, Balabin RM, Zenobi R (2010) Single-cell MALDI-MS as an analytical tool for studying intrapopulation metabolic heterogeneity of unicellular organisms. *Anal Chem* 82(17):7394–7400.

**100** Ghosh S, et al. (2011) Phenotypic heterogeneity in mycobacterial stringent response. *BMC Syst Biol* 5:18.

**101** Davidson CJ, Surette MG (2008) Individuality in bacteria. *Annu Rev Genet* 42:253–268.

**102** Ackermann M (2013) Microbial individuality in the natural environment. *ISME J* 7(3):465–467.

**103** Verbruggen E, Kiers ET (2010) Evolutionary ecology of mycorrhizal functional diversity in agricultural systems. *Evol Appl* 3(5-6):547–560.

**104** Adler J (1975) Chemotaxis in bacteria. *Annu Rev Biochem* 44:341–356.

**105** De Weert S, et al. (2002) Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by Pseudomonas fluorescens. *Mol Plant Microbe Interact* 15(11):1173–1180.

**106** Bay G, et al. (2013) Boreal feather mosses secrete chemical signals to gain nitrogen. *New Phytol* 200(1):54–60.

**107** Song Z, Feldman MW (2013) Plant-animal mutualism in biological markets: Evolutionary and ecological dynamics driven by non-heritable phenotypic variance. *Theor Popul Biol* 88:20–30.

**108** Foster KR, Kokko H (2006) Cheating can stabilize cooperation in mutualisms. *Proc Biol Sci* 273(1598):2233–2239.

**109** Koyama NF, Caws C, Aureli F (2012) Supply and demand predict male grooming of swollen females in captive chimpanzees, Pan troglodytes. *Anim Behav* 84(6):1419–1425.

**110** Wei W, et al. (2013) Supply and demand determine the market value of access to infants in the golden snub-nosed monkey (Rhinopithecus roxellana). *PLoS ONE* 8(6):e65962.

**111** Wernegreen JJ (2012) Mutualism meltdown in insects: Bacteria constrain thermal adaptation. *Curr Opin Microbiol* 15(3):255–262.

**112** Toby Kiers E, Palmer TM, Ives AR, Bruno JF, Bronstein JL (2010) Mutualisms in a changing world: An evolutionary perspective. *Ecol Lett* 13(12):1459–1474.

**113** Kiers ET, West SA, Denison RF (2002) Mediating mutualisms: Farm management practices and evolutionary changes in symbiont co-operation. *J Appl Ecol* 39(5):745–754.

**114** Johnson NC (2010) Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytol* 185(3):631–647.

**115** Sachs JL, Hollowell AC (2012) The origins of cooperative bacterial communities. *MBio* 3(3):e00099–e12.

**116** Morris JJ, Lenski RE, Zinser ER, Loss AG (2012) The Black Queen Hypothesis: Evolution of dependencies through adaptive gene loss. *MBio* 3(2):e00036–e12.

**117** Maughan H, et al. (2006) The population genetics of phenotypic deterioration in experimental populations of Bacillus subtilis. *Evolution* 60(4):686–695.

**118** Ratcliff WC, Denison RF (2010) Individual-level bet hedging in the bacterium Sinorhizobium meliloti. *Curr Biol* 20(19):1740–1744.

**119** Ratcliff WC, Denison RF (2011) Bacterial persistence and bet hedging in Sinorhizobium meliloti. *Commun Integr Biol* 4(1):98–100.

**120** Denison RF, Kiers ET, West SA (2003) Darwinian agriculture: When can humans find solutions beyond the reach of natural selection? *Q Rev Biol* 78(2):145–168.

**121** Schluter J, Foster KR (2012) The evolution of mutualism in gut microbiota via host epithelial selection. *PLoS Biol* 10(11):e1001424.

**122** Bäckhed F, Ley RE, Sonnenburg JL, Peterson DA, Gordon JI (2005) Host-bacterial mutualism in the human intestine. *Science* 307(5717):1915–1920.

**123** Ezenwa VO, Gerardo NM, Inouye DW, Medina M, Xavier JB (2012) Microbiology. Animal behavior and the microbiome. *Science* 338(6104):198–199.