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Short Review

Microbial markets: socio-economic perspective in studying microbial communities

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Abstract

Studying microbial communities through a socio-economic lens, this paper draws parallels with human economic transactions and microbes' race for resources. Extending the 'Market Economy' concept of social science to microbial ecosystems, the paper aims to contribute to comprehending the collaborative and competitive dynamics among microorganisms. Created by a multidisciplinary team of an economist, microbiologists, and mathematicians, the paper also highlights the risks involved in employing a socio-economic perspective to explain the complexities of natural ecosystems. Navigating through microbial markets offers insights into the implications of these interactions while emphasizing the need for cautious interpretation within the broader ecological context. We hope that this paper will be a fruitful source of inspiration for future studies on microbial communities.

Keywords: biological market theory; comparative advantage; evolutionary game theory; spatial economics

Abbreviations

BMT:	Biological market theory
CSR:	Corporate social responsibility
ED:	Evolutionary dynamics
GDP:	Gross domestic product
GET:	General equilibrium theory
RPS:	Rock–paper–scissors

Introduction

Microbial communities exhibit notable similarities with economic markets, showcasing a complex interplay of microorganisms involved in interactions that mirror economic transactions observed in human markets. At the core of these microbial networks lies the fundamental mechanism of resource exchange, where microorganisms collaboratively and competitively 'trade' nutrients, metabolites, and signaling molecules (Kost et al. 2023), forming a dynamic network similar to the commodity trading evident in human markets (Noe and Hammerstein 1994, Toby Kiers et al. 2003, Werner et al. 2014). Within microbial ecosystems, a division of labor emerges where diverse microbes specialize in distinct metabolic functions, contributing substantially to the overall stability and efficiency of the ecosystem (Kost et al. 2023). This specialization underpins central dynamics within microbial communities, marked by instances of cooperation as microorganisms form alliances for resource acquisition, analogous to countries establishing trade partnerships for mutual benefit. Conversely, instances of competition are also evident within microbial interaction, reflecting the struggle for dominance among certain microbial species, similar to companies competing for a larger market share (Foster and Bell 2012). This interplay of cooperation and competition within microbial networks has far-reaching implications for ecosystem dynamics. The specialized functions of different microbial species contribute to the resilience and adaptability of the overall ecosystem (Shade et al. 2012). Like companies focusing on their core competencies, microbial species optimize their metabolic functions, enhancing the efficiency of resource utilization within the community. The resulting network of interdependence and competition among microbial entities mirrors the economic relationships in human markets, with each participant contributing to the overall functioning of the system (Ozkaya et al. 2017).

The 'Market Economy' in social science proposes that economic market agents (humans and institutions) trade things they require, such as goods or services. The conceptualization of microbial communities as biological markets provides a framework that enhances our understanding of their inherent operational dynamics and adaptability. Aligned with ecological and economic principles, this perspective explains the interactions among microorganisms, shedding light on their strategies for resource utilization, cooperation, and competition. Beyond a metaphorical understanding, the exploration of microbial markets examines the mechanisms governing microbial ecosystems, offering profound insights into their implications for broader ecological and human systems. Following Marshall's perspective (Marshall 1920), we see how by leveraging insights from microbial ecology (and its successful models) we can revisit existing economic models aiming to achieve a balanced market ecosystem. Successful examples of research at the intersection of economics and biology include

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for instance recent work on understanding undernutrition in developing economies (Luke et al. 2021).

This paper aims to observe and explain microbial interaction from an economic perspective and advocates that applying market principles to study microbial interactions can be insightful to better comprehend microbial cooperation and evolution and stimulate novel study designs. We mainly focused on microeconomic analysis but did not disregard a macroeconomic perspective, and hence the following country-level trade examples will be used as a parallel in specific sections below. Steamed out of an intensive collaboration between an economist and micro and computational biologists, we aim to provide a comprehensive picture of the advantages and risks associated with employing a socioeconomic perspective on microbial communities. For this paper, we will focus on biological systems involving at least one microbial partner and engage in research questions related to microbial markets. These questions revolve around topics like whether microbes distinguish their trading partners and whether spatial agglomeration plays a role (Meacock and Mitri 2023). This approach of viewing microbial dynamics through the lens of the 'biological market' guides our understanding of the microbial community and cooperation among microbes.

Biological market theory: bridging economic and biological realms

The market economy concept provides a valuable perspective for studying mutualism, the symbiotic partnership among diverse species in an ecosystem. Central to this inquiry is biological market theory (BMT), developed by Noe and Hammerstein (Noe and Hammerstein 1995). Rooted in evolutionary biology and drawing inspiration from the 'comparative advantage' principle of economics, BMT asserts that animals actively participate in cooperative and trading behaviors. Despite the potential for exploitation or cheating, these interactions persist, driven by the comparative benefits that accumulate for participants. Traders in the biological market exchange commodities, including goods (e.g. nutrients, shelter, and gametes) or services (e.g. warning calls, protection, and pollination). BMT serves as a valuable framework for scientists to analyse and interpret cooperative behaviors in the animal kingdom, establishing connections between the natural world and economic systems (Fruteau et al. 2011, Grinsted and Field 2017, Noe and Kiers 2018). Table 1 provides examples of several studies conducted on various animal species, employing BMT as a guiding lens.

A market framework can theoretically be employed for the study of mutualisms if certain conditions for biological markets are met. These conditions encompass: (i) exchanging commodities (goods or services) between individuals, (ii) having at least two distinct classes of traders, (iii) the ability of individuals from at least one trader class to choose or switch partners, and (iv) the existence of individual variations in commodity prices, allowing opportunities for 'outbidding' price competition. Moreover, (v) temporal fluctuations in the supply and demand of these commodities, which can lead to price changes (Noe and Hammerstein 1995), are also typically observed in most markets. These conditions facilitate the application of an economic market framework to explore mutualistic interactions in the biological realm.

In contrast to Smith's argument that 'to exchange one thing for another is common to all men, and to be found in no other race of animals (Smith 1776),' the evolutionary perspective of BMT suggests animals, lacking cognition, participate in 'biological marketplaces' (Noe and Hammerstein 1994, 1995, Toby Kiers et al. 2003). Within ecological systems, animals exchange commodities in the form of goods or services (such as food, grooming, protection, cooperative hunting, or mating opportunities) to enhance their fitness and reproductive success (Hammerstein and Noe 2016). BMT clarifies the occurrence of cooperative interactions among animals, a phenomenon not easily explained by conventional natural selection or theories emphasizing competitive and selfish behaviors. BMT redirects attention to cooperative and mutually beneficial interactions. In biological markets, animals can be perceived as 'traders' capable of assessing the value of various trading partners, making economic decisions, and engaging in transactions by offering valuable resources to the most favorable and reliable partners in exchange for necessities, all to maximize their respective fitness.

The integration of market economic concepts with biological systems provides a premise for exploring the dynamics of microbial communities from a fresh standpoint, upon which the application of micro- and macroeconomic perspectives enhances our understanding of their complexities.

Relevance of micro- and macroeconomics for studying microbes

The application of economic concepts to microbial studies unveils remarkable parallels, particularly when viewed through micro- and macroeconomic lenses. These two branches of economics focus on different scales of economic activities. Hence, analysing microbial communities from these perspectives enables a deeper understanding of their complex dynamics and interactions. On one hand, microeconomics focuses on the behavior of individual agents, such as consumers, firms, and industries, and how their decisions impact resource allocation and prices in specific markets. It examines the mechanisms of supply and demand, production and consumption choices, and market competition to understand how resources are distributed and utilized. Key concepts include marginal utility, opportunity cost, competitive advantage, and market equilibrium, which help to explain how agents interact under constraints (Kolmar 2022). Studying microbial communities using microeconomics would involve analysing how individual microbial species interact, compete for resources like nutrients and space, and maximize their fitness within their environment (Kashtan et al. 2022). For example, consider the competition between bacterial species in the human gut. Here, some bacteria produce antimicrobials to create barriers to entry for rival species, thereby securing more resources for themselves (Woelfel et al. 2024). Through the microeconomics lens, this scenario mirrors how firms might use competitive strategies to dominate a market and optimize their resource allocation for maximum profitability. By applying microeconomic principles, we can study competitive interactions governing microbial ecosystems.

In contrast, macroeconomics deals with the study of large-scale economic factors and phenomena at the level of an entire economy or country. It examines aggregates such as national income, gross domestic product (GDP), unemployment rates, inflation, and government policies to understand the performance and structure of economies as a whole. Macroeconomics seeks to analyse and explain how these variables interact and influence one another, shaping the overall economic environment and determining long-term growth, stability, and development. Through the study of macroeconomics, economists aim to formulate policies that can address issues such as monetary fluctuations, unemployment, inflation, and income inequality on a national as well

Table 1. Examples of findings from literature applying BMT for their analysis.

Agents of biological market	Main findings	Relevant economic principles	Ref
Female sooty mangabey—vervet monkeys	Each female monkey possesses a clear understanding of her value as a grooming partner in the market and knows the level of investment required to receive a satisfactory amount of grooming	Higher demand impacting market value, competition for grooming partners, market information and investment, negotiation and exchange of services, and so on	Fruteau et al. (2011)
Paper wasps	(i) Subordinates have alternative nesting options that provide fitness payoffs as high as their chosen nests but exceed the benefits of solitary breeding. (ii) Having good alternatives outside the group will impact how much help subordinates are willing to offer in raising the dominant's offspring. (iii) Replacing a new floater with an existing helper could not be done easily in the experiment, indicating that rejecting them might incur costs for dominants	Cooperation and collective benefits, competing for better pay-off, external opportunities impacting cooperation, resistance to change, and so on	Grinsted and Field (2017)
Labroides dimidiatus and reef fish	Model system of mutualism where the cleaner wrasse (*Labroides dimidiatus*) chooses its partner	Supply–demand, different pricing, competition for grooming partners, resource allocation, and so on	Bshary (2001)

as global scale (Howitt 1991). In the realm of microbial studies, the principles of macroeconomics can shed light on broader ecosystem dynamics and sustainability (Meacock and Mitri 2023). For example, microbial communities play a crucial role in nutrient cycling, soil fertility, and decomposition processes, which are essential for agricultural productivity. Through the lens of macroeconomics, scientists can assess the economic impact of microbial activities on crop yields, soil health, and ultimately, food security. This illustrates how macroeconomic principles can be applied to microbial studies to enhance our understanding of the economic importance of microbial communities

Both micro- and macroeconomic perspectives offer valuable insights when applied to studying microbial communities, providing different scales of analysis to understand the complex dynamics at play. However, for studying the population dynamics of a microbial community, microeconomics principles can be valuable as they center on the behavior and interactions of individual agents, which mirrors the complex relationships within microbial populations. From resource allocation to competition and cooperation, microeconomic principles provide a powerful framework for studying the complexities of microbial ecosystems.

Furthermore, microeconomics offers insights into the intricacies of competition and cooperation among individual agents, which is essential for understanding the dynamics of microbial communities. Microeconomic principles can be used to explain how certain microbes dominate or coexist, how they respond to changes in their environment, and how resources are distributed among them. For instance, concepts such as supply and demand, utility maximization, and resource allocation provide valuable insights for predicting and analysing microbial behavior in response to various stimuli.

In the pursuit of understanding microbial interactions, emphasizing microeconomic analysis is hence crucial. This approach highlights the importance of focusing on individual behaviors and interactions, without dismissing the relevance of macroeconomic perspectives. By weaving together insights from both micro- and macroeconomic lenses, researchers can paint a comprehensive picture of microbial dynamics, enriching our understanding of these ecosystems. As such, while this paper predominantly focuses on microeconomic analysis, it acknowledges the complementary role of macroeconomic principles for microbial studies.

Microbial market: expanding BMT to microbial population

Microorganisms, too, engage in cooperative actions, interacting with both their hosts and other microorganisms (Cavaliere et al. 2017). While the notion of comparing mutualism to a market is intriguing, it is worth noting that many studies reinforcing this comparison have primarily concentrated on interactions among higher organisms and not microorganisms (Fruteau et al. 2011). This gap in research invites a deeper exploration into the microbial realm, where market-like behaviors emerge despite the absence of cognitive processes. As microbial actions and responses are difficult to monitor and measure, mutualisms involving microbial partners are comparatively underexplored. However, trade deals made by microbial partners surprisingly exhibit similar characteristics as observed in other mutualism instances (e.g. in humans and animals), including competition among multiple partners, trading in the form of cross-feeding, and even the potential to cheat (see Fig. 1). This reflects the microbial population's intrinsic survival drive paired with its opportunistic nature, mirroring the strategic dynamics seen in human interactions.

This scenario sets the stage for evolutionary game theory, a framework offering a distinct perspective to study the complex dynamics of mutualistic interactions within the biological realm (Traulsen et al. 2009). Evolutionary game dynamics bridges the gap between individual actions and broader biological approaches by

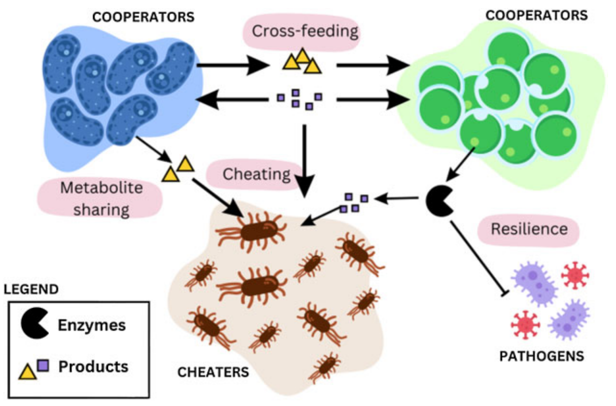

Figure 1. Schematic representation of the microbial interactions, depicting their opportunistic behavior. Cooperators provide products for the whole community by either directly releasing products or secreting enzymes, whereas cheaters directly acquire products from the common pool generated by others without contributing additional labor. Cooperative behavior can involve cross-feeding, metabolite or enzyme sharing, or increasing resilience against pathogens. Figure inspired by Smith and Schuster (2019), Tang (2019), and Figueiredo and Kramer (2020).

applying principles that do not rely solely on rational decision-making. Extending the analysis of decision-making processes into biological markets, evolutionary game theory differs from traditional game theory by challenging the underlying assumption that all players are rational (Dong 2020). This deviation makes it applicable to studying microbial population dynamics and setting grounds for a framework for quantitative population biology (Bak and Rozlach 2020). Like classical and evolutionary game theory, conventional market economies assume cognitive traders as market agents (Smith 1776), but BMT challenges this notion by extending its application beyond animals with simple nervous systems to microbes, which, despite lacking sensory nervous systems, can still exchange information (Noe 2006).

Such exchange of information is crucial, particularly when considering the interactions between pathogens and viruses, whose survival is intricately linked to the viability of their host. During an infection, temperate viruses have two options: either they replicate and thereby destroy the host cell (lytic cycle) or they can become part of the host genome and replicate together with it forming the most intricate relationship between host and virus (lysogenic cycle). Phages, the viruses of bacteria, were found to employ a small-molecule communication system (arbitrium system) for coordinating these two states. For that, a communication-peptide is produced by phages that infect *Bacillus* host cells. This peptide is sensed by further phages and if the concentration is low (small number of infected cells), phages will enter the lytic cycle. If the concentration of the peptide is rising (the majority of the host population consumed) they will enter the lysogenic cycle because otherwise they would eradicate their host (Erez et al. 2017). Interestingly, an established lysogeny of phages can be advantageous for the host, too, like it is e.g. the case for *Corynebacterium glutamicum*. This bacterium contains integrated prophage elements that harbor inter alia the genetic equipment for a defense mechanism against foreign DNA (restriction modification system) (Frunzke et al. 2008, Pfeifer et al. 2016). In this context, phages provide additional defense to the host ensuring not only its survival but also supporting their propagation.

Human-led trade markets rely on cognition to make trade decisions. Unlike traders in the traditional economic market, microbes as market agents borrow, exchange, steal, and cheat; all in the absence of thoughts, however, not in the absence of communication. Whether market agents need to have cognition to lead trade is a question that economists have been exploring (Suchak and Waal 2012). In the neoclassical market, it is argued that economic agents are living breathing rational humans. For example, humans as rational market agents emphasize maximizing their profit (Johnson 2019). In contrast to the neoclassical theory, some supporters of the BMT argue that cognition is not necessary. They believe that the terms of exchanging goods and services can be explained by only considering the current value of the possible partner and the situation at hand (Noe and Hammerstein 1995, Toby Kiers et al. 2003). According to BMT, the focus is on instant gains rather than thinking about future benefits (Brosnan et al. 2010), and they believe that advantageous behaviors can develop without requiring thinking (Noe 2006). However, agents without cognition lack the humane feature of rationalizing their behavior. It is not that they lack input–output functions linking decision problems to choices.

If cognition is not necessary for markets, market systems can be applied to organisms lacking complex nervous systems, such as microbes (Werner et al. 2014, Noe and Kiers 2018). The application of economic market systems to microbial mutualistic interactions serves as a significant test of the robustness of market-based principles as a framework for understanding, cooperation and evolution. The socio-economic trade system provides us with a benchmark to study what an economy looks like when it has been shaped by natural selection for hundreds of millions of years. Uncontaminated by cognition, jealousy, hope, humane instincts, microbes interact with their innate instinct of survival. By studying microbial communities from a socioeconomic perspective, we might learn principles of the microbial market which have been successfully shaped by the 4 billion years of evolution. In the present era of synthetic biology, adopting a microbial market perspective can contribute to an enhanced understanding of the intricate feedback mechanisms between interacting partners and inspire the engineering of novel cooperative interactions. This approach propels our comprehension of microbiology and also advances our knowledge of collaborative dynamics in a broader context. These novel insights, often supported by developed computational models of microorganism interactions (Matuszynska et al. 2022), will support the design and construction of stable synthetic communities by artificially combining distinct microbial species of choice in the future (see synthetic combination of phototrophs with fungi in Fig. 2). As both economics and biology use mathematical models to abstract the complex phenomena they are investigating, the next section will elaborate on how computational research has helped both disciplines gain impetus.

Computational modeling in economics and biology

Economics and biology rely on detailed observations in natural or anthropogenic environments and often explain them with mathematical models simulated on computers. Mathematical modeling encodes the current knowledge about a phenomenon in a form accessible by *in silico* analyses. Through these analyses, researchers generate new hypotheses for the mechanisms behind an economic or biological system, e.g. markets or microbial networks. Additionally, well-validated computer models can serve for prediction-making and, thus, inform political or economic decisions.

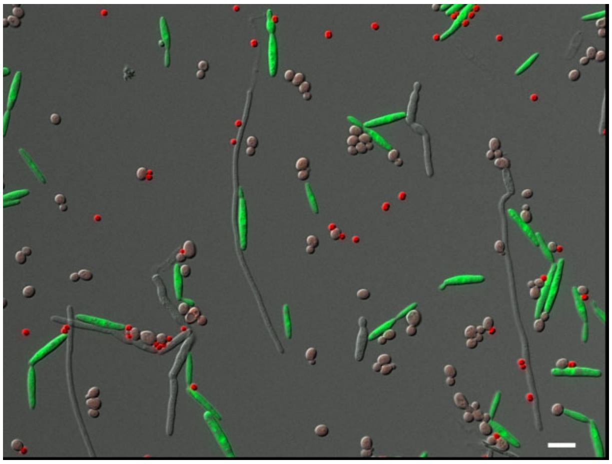

Figure 2. Synthetic combination of microorganisms of choice. Micrograph of autofluorescent cyanobacteria (bright red) and the two fungal model organisms, *Saccharomyces cerevisiae* (light red) and *Ustilago maydis* (green), growing in the yeast form and carrying fluorescent reporters. In addition, unlabeled hyphae of a *U. maydis* laboratory strains are present. The species have been artificially combined for microscopy. Scale bar, 10 μm.

Ranging from linear and dynamic programming used in finding optimal transport routes or analysing job search to Markov chains investigating fiscal policy (McCall 1970, Lucas and Stokey 1983, Simchi-Levi et al. 2014), the field of quantitative economics applies a rich mathematical theory. With this theory, quantitative economics deepens our understanding of the complex human relationships forming our economy. Likewise, computational biology uses theoretical and numerical methods in researching the ecological interactions and evolution of (microbial) populations or the metabolism in cells (e.g. The Economic Cell Collective 2023). Both disciplines share common methodologies, thus offering the potential for expanded knowledge exchange. These exchanges allow, for instance, the mathematical formalization of biological phenomena that were not possible before and provide original angles for new discoveries of governing principles of microbial growth and interaction (Zeng et al. 2021).

For instance, the concept of resource allocation and the corresponding allocation models have been successfully transferred from microeconomics to biology (Molenaar et al. 2009, Dourado and Lercher 2020). In more detail, by extending the resource allocation decision theory into the microbiological world, Mukherjee et al. (2023) used growth law models to discover that nutrient quality reflects resource allocation decisions, and although shaped by evolution in specific ecological niches, these decisions can be quickly adapted.

A prime example in which biology overtook economic principles is evolutionary dynamics (see section "Microbial Market: Expanding Biological Market Theory to Microbial Population"). Initially developed in a purely human-centric context (Neumann and Morgenstern 2007), evolutionary game theory enhances profound knowledge about ecology and evolution by utilizing various forms of mathematical models, see for example (Broom and Rychtář 2022). Evolutionary game theory simulates the dynamic evolution of a certain strategy of a population. Game theory and mathematical economics provide well-studied strategic scenarios, such as Prisoners' Dilemma (Kuhn 2019) or rock–paper–scissors (RPS) (Czárán et al. 2002, Kerr et al. 2002, Neumann and Morgenstern 2007), that can be used further to study the fitness outcomes of interactions between subpopulations in biological

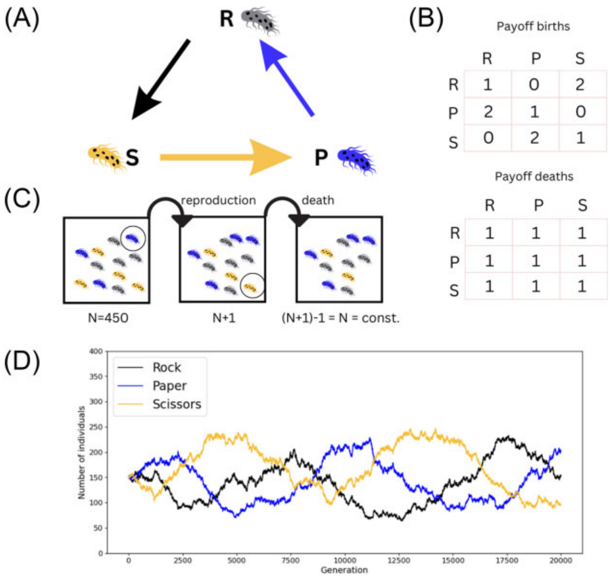

Figure 3. (A) Schematic representation of the RPS game applied to three *E. coli* phenotypes, where each strategy dominates and gets dominated by exactly one other strategy. (B) In evolutionary game theory, each individual's selection for reproduction and death is proportional to individuals' fitnesses calculated based on two separate payoff matrices (here: birth/reproduction and death). The average payoffs of each individual is calculated based on its direct neighborhood in the population (in a 2D game each individual has eight neighbors). (C) The stochastic dynamics is implemented in terms of random birth and death events, like in the Moran process, where in each time a random individual is chosen for reproduction and for death (Bak and Rozlach 2020). (D) Simulated population evolution for given payoff matrices (20 000 generations) using Python package [Py]cess, assuming the Moran model (Bak and Rozlach 2020).

context. For example, finding the Nash equilibrium allows modeling economic behaviors that maximize outcomes for each player regardless if it is a microbe or an economic agent. Although the economic predictions of various strategic scenarios are challenging to be tested empirically (Karlan 2005, Wang et al. 2014, Hoffman et al. 2015), more field evidence supporting game theory predictions emerge (Batzilis et al. 2019), including biological evidence *in vivo* (Kirkup and Riley 2004, Nahum et al. 2011). Similarly, as in social sciences, where RPS game is used as a model system for studying decision-making of human-subjects in noncooperative strategic interactions (Cook et al. 2012, Wang et al. 2014), game theory provides valuable insights into the mechanisms of interaction among *Escherichia coli* strains, suggesting a structured dynamic akin to the RPS model, where each strategy dominates and gets dominated by exactly one other strategy (Czárán et al. 2002, Kerr et al. 2002, Neumann and Morgenstern 2007). In this model, three *E. coli* phenotypes—resistant (R), producer (P), and sensitive (S) strains—engage in a cyclic interaction, where each strain has a predictable advantage over one and a disadvantage against another (Fig. 3A). Specifically, colicin-producing (P) strains kill sensitive (S) strains, which outcompete resistant (R) strains, which in turn out-compete producer (P) strains. Kirkup and Riley (2004) provide experimental evidence suggesting that interactions do not simply lead to the exclusion of one or more strains but rather can promote strain diversity through dynamic equilibria. The antagonistic roles of colicins and potentially other bacteriocins maintain microbial diversity, providing a practical confirmation of game theory predictions in microbial communities. In Fig. 3, we provide a schematic representation of an evolutionary game theory using a RPS game and results of numerical simulations performed in Python using package the [Py]cess, a theoretical framework for scientific simulations with Moran process (Moran 1958), a simple stochastic process describing finite populations (Bak and Rozlach 2020). We believe that availability of such open-source general frameworks for quantitative utilization of evolutionary game theory strategies will contribute to a wider application of these models to studies of microbial community formation and dynamics.

Biology contributed to mathematical economic theory as well by inspiring genetic and evolutionary algorithms (Goren et al. 2010, Drachal and Pawłowski 2021). These algorithms are frequently used to solve problems in operational research and supply chain management, e.g. in Altiparmak et al. (2006). Evolutionary computation is not limited to operational research. Another application of genetic algorithms is finding the best regression model and parameters to forecast economic agents' expectations for the development of macroeconomic variables, such as a country's GDP (Claveria et al. 2019). Researchers can use these regression models to investigate the effects of global crises. Additionally, research indicates that incorporating biological input might be critical for machine-learning approaches to economics. Machine learning algorithms that use biological-inspired optimization procedures have been found to be better suited for economic problems than other machine learning techniques not making a connection to how biological organisms are formed by natural selection (Lazebnik et al. 2023).

The biological theory of evolution is increasingly (with care) being applied to understanding human behavior as economic and political agents (Witt 2015). This connection led to disciplines such as evolutionary economics. We can distinguish between a broad and narrow use of evolutionary theoretical concepts for describing economies.

In a broad sense, any system that adapts to changing conditions can be described using evolutionary terms. An example is the adaptation of economies viewed as dissipative structures to external factors. Dissipative structures are dynamic systems far from equilibrium that need constant energy and material input to be maintained. Mathematical techniques from dynamical system theory can describe how economies, as dissipative structures, adapt and change their basin of attraction. A basin of attraction is a set of (initial) system (here economic) states from which a dynamic system would converge to an attractor (a strict convergence, however, to an attractor is not required in dissipative systems). External factors (environmental conditions that lead to resource limitations and, thus, new prices of goods) can change the numbers, shapes, and locations of the basins of attraction in the phase space of the system and the economy will follow another dynamic accordingly. This adaption (different dynamic corresponding to changes in the phase space) can be compared with evolution. However, care must be taken since evolutionary terms mostly speak of populations and not of a single entity, such as an economy [see Heinrich (2017) for a broader discussion].

The narrow approach to applying evolutionary concepts in economics is to treat an economy as a population of companies that evolve through imitation and innovation (Heinrich 2017). Using agent-based models, evolutionary economic approaches could describe economic growth and include insights into population dynamics of resources (Geisendorf and Klippert 2022) or human behavior in their simulations (Heinrich 2017).

Other usages of biological thoughts have been critical for finding a production function of agronomic output in connection to studying the profitability of farming and fishery (Tschirhart 2012). Biology helps to choose the right function that is essential for determining the production of goods and their value on the corresponding markets.

Interpreting microbial communities in the context of the microbial market will increase the easy interdisciplinary exchange between both biological and economical, computational communities by finding a common language that facilitates collaboration.

The fact that microbial community members exchange metabolites encourages comparing microbes with economic agents on markets. The following section elaborates on how microbial communities can be described as biological markets using well-known economic concepts, such as cooperation and competition.

Microbial communities as biological markets and microbes as economic agents

A substantial portion of the Earth's microbial life thrives within complex communities, where metabolic exchanges are crucial. Microbes participate in the trading of essential resources, including a variety of metabolites such as essential amino acids, sugars, fatty acids, and coenzymes, to facilitate their growth. When both interacting microbial partners have a say in whether they want to cooperate or not, it is similar to how humans make choices in markets through trade (Noe and Hammerstein 1994, 1995). Therefore, in this section, we will approach microbial communities as biological markets and view microbes as economic agents, aiming to explore their dynamics of cooperation and competition for metabolites in pursuit of growth or survival. We have drawn parallels between the economic markets and microbial markets in Table 2 and provided several examples from the literature where microbes are treated as economic agents in Table 3.

A prime example of a very resilient microbial marketplace is lichens—a symbiotic association between different fungi (the mycobiont) and photosynthetic partners represented by algae or cyanobacteria (the photobiont; Fig. 4). These symbiotic associations have been proven evolutionary successful and survive under harsh conditions, exemplified by the fact that lichen even grow in the slightest cracks of pavement or on rocks, and endure extreme environmental conditions (Oksanen 2006). Since lichen cannot be grown in the laboratory by simply mixing single partners, research mostly relies on studying lichen isolated from nature. It is well established that the photobiont converts sunlight and CO_2 to assimilates. According to the nutritional model, either glucose or polyols are then put onto the marketplace and are used to sustain the mycobiont's growth. In turn, the mycobiont provides shelter and protection for the photobiont, for example enhancing the resistance against UV, predators, and drought (Nazem-Bokaee et al. 2021, Pichler et al. 2023).

Several studies have already applied economic principles in microbiome science, contributing to a comprehensive understanding of microbial interactions and ecological dynamics. Werner et al. (2014) have expanded the framework of BMT to assess its relevance to evolutionary biologists studying microbes. The authors have explored different economic strategies that microbes use to enhance their success in these biological markets. They have shown that embracing an economic market framework provides a valuable tool for making precise and intriguing predictions about microbial interactions. This includes aspects like the development of partner discrimination, strategies for resource accumulation, choosing between specialized and diversified

Table 2. The table exhibits a comparison of an economic market to a microbial market from the lens of key market dynamics.

Key market dynamics	Economic market	Microbial market
Agents	Human, institutions, government, trade unions, and so on	Microbes
Goal of trade	Maximize profit, economic growth, market expansion, diversification, and so on	Maximize biomass and growth rates (short-run), survival and resilience (long-run)
Commodities	Desired goods and services	Goods (metabolites) and services (growth, resistance, reproduction, and protection from predators)
Decision-making instinct	Rationality, cognition, greed, selfishness, egoism, irrationality, altruism, information asymmetry and uncertainty, and so on	Survival and fitness advantage
Determinant of purchasing capacity	Price of the good, income, savings, credit and loans availability, inflation rate, and so on	Metabolic capacities, energy cost, and signaling
Criteria for choosing partners	Price, quantity and quality, and proximity	Compatibility, gained benefit, complementarity, natural selection, and niche

Table 3. Findings from existing literature reflecting microbes as economic agents.

Agents of microbial market	Main findings	Relevant economic principles	Ref
Arbuscular mycorrhizal fungi—plant mutualism	Plants and fungi have the capacity to distinguish between good and bad trading partners and respond by preferring interactions with partners that offer more advantageous exchanges	Partner selection and market preferences, resource allocation and efficient transactions, maximizing profit, risk assessment and adaptability, and so on	Noe and Kiers (2018)
Mycorrhizal fungi	Inequality shapes trade patterns within fungal networks, as fungi capitalize by prioritizing resource movement to high-demand areas	Exploitation of market disparities, resource distribution, supply and demand, trade and exchange mechanisms, and so on	Whiteside et al. (2019)
Mycorrhizal fungi and host roots	The fungus regulates phosphorus transfer to host plants by adjusting its allocation strategy based on resource availability. During resource scarcity, it shifts phosphorus transfer from alternative pools closer to the root. Conversely, during resource abundance, it stores surplus phosphorus, releasing it when root demand increases	Supply and demand, scarcity, market equilibrium, adaptive efficiency, savings and investment, risk management, economic resilience, and so on	Padje et al. (2021)
Lichens (fungi and algae)	Lichens, through symbiotic relationships between fungi and algae, demonstrate a market, where polyols play a critical role in resource exchange. This dynamic reflects a multiplayer marketplace of rewards and penalties, driving symbiont selection and diversification	Market diversification, resource exchange, symbiotic mutualism, competitive and cooperative interactions, and so on	Kranner et al. (2022)
Lichen symbiosis	Lichen symbioses illustrate a complex marketplace of goods and services exchange between fungus and phototrophs, enabling lichens to thrive in diverse and extreme environments by utilizing mutual benefits and adaptations for survival, such as desiccation resistance and nutrient exchange	Resource Allocation and efficiency, adaptation to environmental stress, specialization, trade-offs, and so on	Spribille et al. (2022)

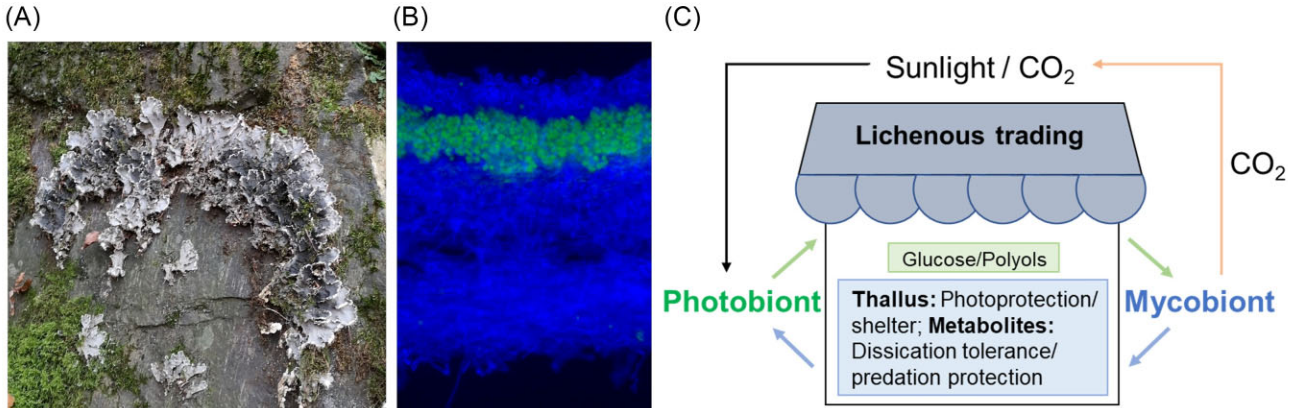

Figure 4. (A) Picture of a Peltigera lichen growing on a rock close to Dusseldorf, Germany. (B) Microscopic view on the structure of a lichen in a thallus intersection. Blue, mycobiont stained with calcofluor white; green, chlorophyll autofluorescence of the photobiont cells. (C) Simple schematic representation of lichens as a microbial marketplace, where trading of different goods and services is exhibited to support the resilience of the symbiotic association.

mutualistic services, and the importance of spatial configurations such as groups and collaborations. As a result, studying the evolutionary dynamics of microbial systems holds great potential. Applying BMT can efficiently shape and guide research in this field by highlighting the strategic investments microbes make in different conditions.

Tasoff et al. (2015) have expanded BMT by constructing a framework grounded in the principles of general equilibrium theory (GET) from economics. According to GET, markets and other economic systems dynamically evolve and interact with each agent independently optimizing their consumption, production, and exchange decisions. This optimization process ensures there is no excess supply or scarcity of goods at the current price. Applying this framework to microbial ecosystems engaged in resource exchange allows the forecasting of population dynamics. The study provides insights into metabolite production, allocation, and the immediate growth benefits associated with microbial trade; grounded in the growth requirements, metabolic abilities, and intercellular transport rates of each microbial species. These insights are relevant for understanding microbial ecology and engineering synthetic communities.

Microbes generate essential metabolic resources for survival, with some escaping into the surrounding environment, creating what is termed 'leaky microbial trade.' Other microbes utilize these 'leaked' resources, adapt their metabolic production accordingly, and influence the resource pool available to all. Kallus et al. (2017) have examined a model that explores the coevolution of metabolite concentrations, production regulation, and population frequencies. In this scenario, two types of cells produce two distinct metabolites (Kallus et al. 2017). Within this model, the authors point out paradoxes where increased efficiency in metabolite production paradoxically may decrease an organism's population frequency and interventions to enhance growth rates can result in lower overall growth. These paradoxes show the intricate dynamics that emerge within even the simplest microbial economies, demonstrating that, akin to human economies, microbial ones are opportunistic, with 'free riders' lurking around the corner.

Despite the complex dynamics observed in microbes, the endurance of microbial networks relies on their inherent resilience. In traditional trade markets, dominance by a single entity, such as a large corporation like Amazon, can lead to market instability. This is because too much dependence on one entity makes the market vulnerable to any issues that affect that entity (Rikap 2022). On the other hand, microbial communities thrive on diversity and resilience. This resilience is akin to the economic stability observed in Germany during the 2008 financial crisis because the country had many medium-sized companies that were less reliant on credit and more adaptable to change (Schindler 2013). Similarly, in microbial markets, resilience is not about achieving immediate dominance or maximizing biomass production in the short term. Instead, it is about ensuring long-term stability and survival through regulated cell division and resource sharing. For example, microorganisms in extreme environments, such as those found in high-altitude mountainous regions, demonstrate remarkable resilience by adapting their growth rates, with cell division for instance in snow samples taking up to about 100 days (Sattler et al. 2001). This slow growth rate is an approach not for immediate expansion, but rather for maintaining stability and longevity in harsh conditions. Such microbial survival instinct highlights the importance of resilience in biological markets. It points out that achieving an optimal state is not merely about rapid growth or dominance, but about creating a balanced and sustainable ecosystem where various entities coexist and cooperate. Integrating this perspective of microbial resilience offers valuable insights into how economies might be structured for long-term stability and sustainability, emphasizing the role of diversity and adaptability over dominance.

Even though the microbial world has evolved much longer than the human world and thus well-established communities such as soil or gut microbiomes are considered more balanced and more resistant to slight disturbances, similar crises like the mentioned financial crises are happening among them. Various pathogen attacks can drastically disturb the composition of the microbiome, leading, in the most severe case, to death of the host (Gagliardi et al. 2018). Interestingly, recent evidence shows that our own microbiome continues to live on after our death. Gut bacteria, especially a class of microbes called Clostridia, spread through the organs and digest us from the inside out in a process called putrefaction (Keenan et al. 2023). Crises occur steadily in the microbial world on a less drastic scale, and those microbes have to adapt to new environments and new conditions of trading constantly. There are drastic natural influences for crises on the microbial market but also human-made ones. A stable phototrophic consortium that is trading nutrients based on the photosynthetic activity of the photobionts are heavily impacted by the immediate lack of sunlight for example. Therefore, we believe that it is not crucial for the evolutionary scale of microbial and human markets to be entirely identical in order to make a comparison.

Building upon the exploration of microbial resilience and its parallels with economic principles, the following section transitions to examining the impact of location on microbial interaction and growth across varied systems.

Spatial economics of microbial interaction

One pivotal question within the market economy revolves around the geographical concentration of economic trade. Where will firms and industries locate, relocate or stay? The spatial positioning of economic endeavors holds significance not only in terms of resource mobilization but also in profit generation, import–export, public expenditure, urbanization, and pollution (Hanson 2001). Understanding the rationale behind geographical concentration is instrumental, as it sheds light on key aspects of international trade and growth.

Building upon this spatial economic context, the Heckscher–Ohlin model, known as factor-endowment theory, introduces the perspective that the production location is determined by a nation's abundant factors. The country tends to export goods that rely on factors of production that are relatively abundant nationally, while it imports goods requiring factors that are scarce domestically (Negishi 2001). Despite assuming identical production functions across all nations, the model posits that for industry localization, the production costs, based on prevailing factor prices, must be lower than in other regions or countries. In essence, certain factors are more cost-effective domestically, thereby enhancing the return to scale.

Further exploring the implication of proximity, one rationale for firms' spatial agglomeration is rooted in location specific externalities. Positive externalities are beneficial consequences of activities that spill over to other entities that are not directly involved in those activities. This is particularly evident in efficient transportation costs that create location-specific externalities. As the impact of external effects weakens with distance, there is a strategic incentive for agents to cluster together, thereby reaping an enhanced return to scale (Hanson 2001).

Such an engagement in the exchange of information to enhance collective fitness also concerns microorganisms. Bacterial communication is essential for coordinating behaviors that require a 'critical mass,' such as the production of bioluminescence or the colonization of a host during infection. Bacterial quorum sensing describes the underlying principle, wherein bacteria release signaling molecules called autoinducers into their environment. As the bacterial population density increases, the concentration of these molecules rises, allowing bacteria to sense their collective numbers and orchestrate synchronized gene expression for specific behaviors, including biofilm formation or virulence (Mukherjee and Bassler 2019). *Staphylococcus aureus* infects the human host through, e.g. a defective skin barrier, establishing a biofilm when found at low cell densities. Upon getting high cell densities, the concentration of a constantly expressed autoinducer exceeds a critical value, triggering the bacterial cell population to stop the biofilm formation while starting the expression of colonization and virulence factors, to finally occupy within the host (Yarwood and Schlievert 2003). Interestingly, quorum sensing also allows interdomain interactions between bacteria and viruses (Duddy and Bassler 2021) or also bacteria and human cells (Wu and Luo 2021) demonstrating its significant fitness relevance in diverse contexts.

Echoing the advantages of spatial agglomeration, urban and regional economists emphasize the link between scale economies, knowledge spillover, and geographical concentration. Henderson (2003) posits that agglomeration economies benefit from positive spillovers among firms colocated in the same geographical area. While individual firms operate under perfect competition and perceive constant returns to scale, the aggregation of economic activities generates externalities that enhance the productivity of all firms within a specific industry sharing a common geographical location. Marshall (1920) suggests that the geographic clustering of firms fosters learning and the exchange of ideas among agents. The presence of localized externalities implies that firms exhibit a preference for proximity to substantial agglomerations of other firms within their industry or related sectors. This leads to the emergence of an urban hierarchy, wherein cities specialize in different industries, and the size of cities is dictated by the magnitude of their respective export activities. In this way, the concentration of industries enhances the productivity of all firms within the same local industry, while the clustering of labor increases the productivity of local workers, irrespective of their specific industry.

Silicon Valley exemplifies how a tech cluster fosters a dynamic environment for innovation. The proximity of tech giants like Google, Apple, and Facebook attracts skilled professionals and fosters a culture of knowledge sharing, competition, and collaboration (Atkin et al. 2022). This concentration of talent and resources drives innovation, drawing in entrepreneurs and reinforcing Silicon Valley's position as a global tech hub. Consequently, the region benefits from positive externalities of spatial agglomeration, such as a rich pool of skilled workers, shared infrastructure and increased productivity, making it an attractive destination for tech companies and professionals.

Microbes live in densely packed, spatially structured communities. Hence, the question arises: how does spatial structure affect microbial behaviors? The structured environment of biofilms represents a ubiquitous feature of microbial life. Biofilms are defined as aggregates or consortiums of cells sticking to each other embedded in an extracellular matrix. This biofilm barrier can support collective protection against environmental issues, like antibiotics, predators, or the human immune system. For the human pathogens *E. coli* or *Pseudomonas aeruginosa* it was shown that a larger size of the biofilm-associated bacterial aggregates is beneficial to overcome the elimination through engulfment (phagocytosis) by human immune cells (leukocytes), compared to an independent, lone cell (Alhede et al. 2020). Beyond that, the human pathogen *Vibrio cholerae* can form biofilms on the surface of human immune cells, which enables a collective killing of these due to a high local concentration of a secreted toxin (hemolysin), and thereby escaping the host immune response (Vidakovic et al. 2023).

Regarding spatial structure, the mentioned lichens exhibit a unique morphology, where fungal hyphae form a complex network, known as the thallus, that encases and interacts with the photosynthetic cells of the photobiont and provides a structural scaffold and shelter. This close integration results in a composite organism with distinct layers, providing an efficient mechanism for the described nutrient exchange and environmental adaptation (Pichler et al. 2023).

Comparative advantage: an insightful concept for studying trade, specialization, and cooperation

One of the most valuable takeaways for biologists from the field of economics is the concept of comparative advantage. According to the classical Ricardian model (Ricardo 1821), countries benefit from trading rather than pursuing complete self-sufficiency. He advises nations to specialize in goods with a comparative advantage, determined by a low opportunity cost (the value of what is given up). This strategic focus on efficiency in production allows countries to participate in international trade, exchanging their specialized goods for those with higher opportunity costs. Ultimately, engaging in trade between entities or nations enhances overall output and consumption beyond what domestic activities alone would achieve.

Comparative advantage finds a compelling parallel in microbial communities, where mutually beneficial trade relationships can emerge when individual species face limitations in independently generating essential resources. For instance, in the absence of trade (autarky), each microbial species expends a significant portion of its resources to produce metabolites with low productivity. However, with trade, species can acquire these less efficiently produced metabolites from their microbial partners, allowing them to allocate more resources to producing the metabolites they excel at. This role optimization enhances overall productivity, benefiting the entire microbial population. Given the diverse metabolic capabilities of different microbial species in a community, the principle of comparative advantage likely plays a key role in shaping microbial population dynamics by influencing the exchange of various metabolites (Tasoff et al. 2015). This concept of specialization and exchange in microbial ecosystems serves as a biological mirror to the economic principle of comparative advantage, illustrating how even in nature, entities can derive mutual benefit from focusing on their strengths and relying on others for their weaknesses.

Transitioning from this ecological form of economic theory, the Black Queen Hypothesis further exemplifies the principle of comparative advantage through the lens of evolutionary biology. It posits that within a microbial community, certain members may evolve to lose the ability to produce specific chemicals or resources that are essential for their survival but costly to produce. These resources, when produced by other community members and released into the environment, become available for all, including those who no longer produce them. This process of reductive evolution—losing the genes for costly functions when they are unnecessary—mirrors the economic strategy of outsourcing less efficient production to partners with a comparative advantage (Jeffrey Morris et al. 2012, Jeffrey Morris 2015).

Thus, the Black Queen Hypothesis not only helps to explain the efficiency of specialization within microbial networks but also highlights a striking parallel to the benefits of trade and role optimization advocated by comparative advantage. By forgoing the production of certain metabolites, these microbes conserve energy and resources (Jeffrey Morris et al. 2014), which can then be redirected toward functions they perform more efficiently. This strategic reduction and niche differentiation enhance the community's overall productivity and resilience, demonstrating how principles of comparative advantage can manifest in both the economic and biological realms to drive mutually beneficial relationships and specialization.

Among microbial communities, it is frequently observed that several organisms do not synthesize particular metabolites essential for their growth (auxotrophy), but rather rely on cross-feeding (Yu et al. 2022, Kost et al. 2023). It was shown that such cross-feeding is less constricting but rather broadens the metabolic niche space of interplaying bacterial populations (Ona et al. 2021), comparable to Ricardo's numerical example (Ricardo 1821). In the fermented milk-drink kefir, obligate metabolic interactions between several microbial species enabled their long-term coexistence. The dominant species, *Lactobacillus kefiranofaciens*, can not grow alone on milk but relies on nutrients provided by other members of the community. In turn, it contributes to establishing a polymeric matrix that improves the survival of other members of the collective (Blasche et al. 2021).

The next section of the paper addresses the context in which microbes are producing public goods and cooperating for collective fitness at the cost of their resources and energy.

Interpretation of altruistic microbial interactions through the socio-economical lens

Depending on environmental conditions and selective forces, microbial species may maximize either their relative abundance or the community's growth rate (Kallus et al. 2017). For instance, let us consider a scenario involving the race of carbons within the microbial communities. Depending on the method of sucrose digestion, the microbial species are divided into subgroups. The public metabolizers generate glucose by secreting invertase, an enzyme catalysing the external breakdown of sucrose into glucose and fructose in the common pool. On the other hand, cheaters simply exploit available glucose from the common pool without contributing to the enzyme (Gore et al. 2009, Chen et al. 2021).

This scenario is perplexing for economists, as it contradicts profit maximization and leads to questions: Why do the public metabolizers generate nutrients for others at the cost of their enzymes and energy? Do these public metabolizers have a selfless concern for others within the community? As microbes lack complex emotions and consciousness, what drives them to conduct such altruistic initiatives? Can it be that the presence of cheaters impacts the overall fitness and survival of the microbial ecosystem, including the public metabolizers?

Corporate social responsibility (CSR) projects of firms offer a valuable analogy to interpret the altruistic involvement of microbes. CSR involves a company's philanthropic actions for positive social impact, environmental sustainability, and improving the well-being of stakeholders beyond its immediate financial gains (Maon et al. 2021). Such CSR activities go beyond a company's legal obligations, embodying a commitment to contribute positively to society, akin to 'corporate citizenship' (Kumar et al. 2022). In the digital age, technology giants (e.g. Google, Amazon, and Facebook) have come under scrutiny for their aggressive market strategies, raising concerns about monopolistic behaviors and market dominance (Rikap and Lundvall 2022). For example, Google's acquisition of Waze, a competitor to Google Maps, highlights the company's strategy to consolidate its position in the digital mapping and navigation sector (Demers and Yemen 2017).

Amidst criticism, these corporations allocate profit to CSR projects, demonstrating their commitment to utilizing their technological strengths and resources for public benefit (Maon et al. 2021). Google, for instance, leads in environmental sustainability, achieving carbon neutrality in 2007 and matching 100% of its global electricity use with renewable energy purchases since 2017 (Carbon-free energy). In addition, Google's 'Grow with Google' program exemplifies using its resources to offer educational opportunities, free training, and tools to help people grow their skills, careers, or businesses (Get the required skills for the changing landscape). This program is particularly aimed at communities that are under-represented in the technology sector, thereby addressing social inequalities and enhancing workforce diversity.

This commitment to social responsibility prompts a crucial question: Why do corporations invest in CSR, allocating a portion of their profits to community welfare, and more importantly, what do they gain from such endeavors? In the globalized corporate landscape, where national boundaries blur, technological advances and competition have condensed time and bridged distances. In this evolved corporate scenario, businesses are keen on enhancing their profit management and risk mitigation strategies, along with safeguarding their brand reputation. Globalization has also intensified the competition for acquiring talented employees, securing investments, and winning consumer loyalty. The way a company engages with its employees, serves the community, and presents itself in the marketplace is pivotal for ensuring its long-term business viability. Engaging in CSR projects strengthens a company's image and boosts employee morale, fosters customer loyalty, and ultimately, increases market demand for its products (Wang et al. 2015). Therefore, engaging in community-focused initiatives is not just philanthropy but a strategic investment for long-term profitability in today's global market.

In microbial markets, the behavior of public metabolizers, who partially privatize glucose while sharing the remainder with their community, mirrors CSR practices in the socio-economic context. This raises the question: Do cheaters occupy a crucial niche within microbial community dynamics? Consider the fermented food scenario involving *L. kefiranofaciens*, which cannot grow alone in milk. It is provided with energy and several essential metabolites from other species in kefir and with that becomes the dominant species within this community. At first glance, this behavior may seem purely parasitic. However, a deeper investigation reveals that indeed, the establishment of a stable community in kefir relies not only on the cheating of *L. kefiranofaciens*, but in turn, this bacterium generates a beneficial polymeric matrix. This guarantees the survival and the reproduction of the further metabolite- and energy-providing bacteria within the community (Blasche et al. 2021). Within microbiomes, several interactive networks can be found, exchanging metabolites, energy, and further to contribute to a collective fitness and from a broader perspective, this can be concluded as cooperative.

Understanding these microbial interactions offers valuable lessons about the broader principles of economics and the importance of holistic analysis. In both economics and microbiology, analysing a single factor in isolation fails to capture the complete picture. A comprehensive evaluation of all elements and demands within a community is necessary to grasp how it functions effectively. Such an approach reveals the complex network of interactions and dependencies essential for success and survival, applicable to both natural ecosystems and economic systems.

Hence, rethinking the community assembly through a socio-economic lens can be insightful in comprehending coexistence and collective fitness in the natural ecosystem.

Risks of employing economic principles to study biological science

While employing economic frameworks in biology can offer valuable insights and a structured analytical approach, there are inherent risks in extending economic concepts to the complexities of biological systems.

Linguistic risks in interdisciplinary research

Merging concepts from other disciplines often entitles borrowing new terminology. While such terminology may seem convenient due to its familiarity, it can lead to confusion or misconceptions, especially if the borrowed term holds different meanings or connotations in its original context. The risk of misinterpretation arises from the inherent differences in conceptual frameworks and terminologies across disciplines. In Table 4, some examples of shared vocabulary with different meanings in their respective disciplines have been provided. This comparison highlights the importance of recognizing context-specific meanings when encountering shared terminology across interdisciplinary studies.

The tendency to repurpose existing words in novel contexts likely arises from the adaptability and flexibility of language (Gibson et al. 2019). Language is a dynamic and evolving system, and speakers often creatively reuse words to convey new ideas or adapt to changing circumstances. This linguistic phenomenon allows for a more efficient and resourceful communication system, as speakers can draw on familiar terms to express novel concepts. Additionally, the reuse of words in different contexts facilitates the evolution of language over time, contributing to its richness and versatility (Piantadosi et al. 2012). Studying various papers in economics and biological science, we have observed that both fields employ similar terminologies, yet these terms carry distinct meanings. For example, the term 'public good' is commonly used both in economics and biological science, yet it carries different definitions within each discipline (Table 4). In economics, a public good is characterized by its nonrivalry and nonextrudability nature (Candela and Geloso 2019), meaning it can be consumed by anyone without diminishing its availability to others. In contrast, within the biological context, a public good refers to a resource or trait that benefits all members of a community (Ozkaya 2017), irrespective of individual contribution. On the other hand, the economic definition of a common good is one that is both rivalrous and nonexcludable (Crespo 2016). This distinction in the definition of 'public good' highlights the need for accuracy and contextual understanding in interdisciplinary conversations, ensuring that common terminology enhances rather than obscures the clarity of communication.

Risk of misinterpretation through anthropomorphism

Economics, as a discipline, is centered around human behavior, markets, and societies. Using economic principles to study microbial interactions may impose an anthropocentric bias by assuming that microbes think and act like humans. When we apply economic jargon like 'exchange' or 'negotiate' to microbes, it unintentionally anthropomorphizes them by attributing human characteristics to nonhuman entities. Microbes and plants follow survival instincts and evolutionary patterns, not human-like conscious decision-making or economic reasoning. This anthropomorphic lens can mislead us into oversimplifying microbial behavior, ignoring the complex biochemical and ecological mechanisms that underlie these interactions (Mota-Rojas et al. 2021).

The example of quorum sensing demonstrates how using economic concepts to describe microbial behavior can lead to misunderstandings about the nature of microbial life. Bacteria communicate through these chemical signals to coordinate

Table 4. A list exhibiting shared vocabularies having different meanings in economics and biological science.

Terms	Economics	Biological science
Public good	A good that is nonexcludable and nonrivalries (Candela and Geloso 2019), meaning individuals cannot be excluded from its use, and usage by one agent does not diminish its availability to others. Example: public road	Often refers to molecules produced by an individual that become available to other neighboring individuals (Ozkaya et al. 2017); the produced good benefits the entire population or group, enhancing the survival and reproduction of individuals, but their acquisition by one agent diminishes the overall availability
Common good	The produced good benefits the entire population or group, enhancing the survival and reproduction of individuals, but their acquisition by one agent diminishes the overall availability (Crespo 2016)	Common good and public good—these terms are used interchangeably in biology. It refers to resources or benefits that are shared by a community (Borges and Santos 2021, Morabia 2020)
Fitness	Effectiveness of a strategy or decision in a competitive market (Ma et al. 2022)	Although numerous definitions of fitness have been introduced (Allen Orr 2009), the broad and general idea behind an organism's fitness involves the relative reproductive success and contribution of genes to future generations, determining an organism's evolutionary success in its environment
Demand	The desire for a product or service, coupled with the ability and willingness to pay for it (Tin 1999)	The ecological need for a specific resource or environmental factor. Coupled with the term of supply, accurately describes the characteristic of self-regulation of metabolic systems (Christensen et al. 2015, Matuszyńska et al. 2019)
Capital	Refers to the financial asset which is an input for the production (Lovchikova and Matschke 2024)	Often used to describe the accumulated resources a species has for survival and reproduction, such as energy reserves or genetic diversity

behaviors such as biofilm formation and the production of virulence factors, contingent upon their population density (Yarwood and Schlievert 2003). If we describe quorum sensing using economic terms, it might sound like bacteria are 'negotiating' their collective actions or 'making agreements' based on the information exchanged. However, this description anthropomorphizes the bacteria, implying a level of conscious decision-making that does not exist. In reality, quorum sensing is a biochemical process driven by evolutionary pressures, not by individual or collective 'decisions' in a human sense. Bacteria respond to chemical cues in their environment in a way that has been shaped by natural selection to benefit their survival and replication, without any awareness or intentionality.

Instead of leaning on popular jargon, investing time in studying primary literature is vital for interdisciplinary studies. In this process, comprehending the principles and assumptions within specific examples from one field before applying them to another is essential. This approach ensures a more thorough and precise exploration of interdisciplinary connections.

Impact of the underlying assumptions

When exploring interdisciplinary studies, it is important to avoid oversimplifying different concepts. For instance, let us take the well-known economic principle that asserts that as the price of a product rises, the quantity demanded tends to decrease and vice versa. However, 'The Law of Demand' is more complex than this simplified idea. The fundamental assumption underpinning this principle is that no other factors, aside from the product's price, are changing. Therefore, if we overlook the critical underlying assumption of maintaining all other factors constant, it can result in errors in predicting consumer behavior and market dynamics. Moreover, external economic factors such as changes in income, prices of related goods (substitutes and complements), and expectations about future prices can also significantly affect demand. These factors highlight the interconnectedness of economic variables and the need for a more comprehensive analysis that goes beyond simplistic models.

In microbial studies, examining multiple factors influencing each other is crucial. For instance, gene regulators with overlapping gene repertoires respond to various signals, showcasing the adaptability and resilience of microbial life. The interplay of signals and regulators highlights the complexity of microbial gene regulation, emphasizing the need for a holistic view to understand microbial behavior and adaptation.

This can also be an issue for microbial studies. Sometimes it is not only one specific factor that we look at, but further factors influencing each other. For example, several gene regulators with an overlapping repertoire of regulated genes incorporate several different signals. The complexity here lies not only in the number of factors involved but in how seamlessly they interact, highlighting the adaptability and resilience of microbial life. This interplay of multiple signals and regulators illustrates the depth of complexity in microbial gene regulation, emphasizing the importance of a holistic view to truly grasp the subtleties of microbial behavior and adaptation.

Learnings from microbial studies: insights for economists

Alfred Marshall, known as the father of evolutionary economics, once wrote that 'the Mecca of the economist lies in economic biology rather than in economic dynamics (Marshall 1920).' By this, Marshall emphasized the profound potential that lies in examining biological processes to understand economic phenomena. His assertion encourages economists to look beyond human activities and dive into biological systems because they offer rich, naturally occurring examples of complex interactions, adaptive behaviors, and evolutionary strategies that mirror economic activities. Microbial studies, for instance, reveal complex systems of cooperation and competition, resource allocation, adaptation, and systems dynamics. In microbial communities, organisms engage in mutually beneficial resource exchanges, akin to economic trade, and compete for scarce resources, similar to market competition. These microbial behaviors provide a natural laboratory for understanding fundamental economic principles in a simplified and observable form in the biological free market.

Marshall's encouragement for economists to explore biology is rooted in the idea that economic systems are not static but constantly evolving and adapting, much like biological systems (Marshall 1920). By studying how microbes optimize resource use, develop resistance mechanisms, and form cooperative consortia, economists can gain insights into how human economies might adapt to changes, innovate in the face of scarcity, and organize for collective benefit (Farmer 2002). By drawing parallels with microbial systems, economists can identify dynamic processes that shape the growth and resistance of economic entities. To build on this microbial perspective, it is essential to consider both narrow and broad perspectives within evolutionary economics. The narrow approach, which draws direct analogies to genetic evolution (Heinrich 2017), treats firms as populations that exhibit diverse routines, technologies, and strategies, subjected to forces of selection and diversity generation. This method leverages established findings from evolutionary biology, offering a structured framework to understand how firms adapt and evolve (Heinrich 2016). For example, just as biologists study the survival of the fittest among species, economists can study which business strategies lead to the survival and growth of firms.

Conversely, the broader approach expands the scope by considering single adaptive entities such as institutions or entire societies, rather than focusing solely on populations (Heinrich 2017). This perspective allows for a more flexible understanding of economic evolution, accommodating a wider array of adaptive behaviors and evolutionary processes. By synthesizing narrow and broad concepts of biological evolution, economists can develop a more thorough view of economic systems, enhancing our understanding of economic dynamics and fostering the development of sustainable economic strategies.

Integrating insights from microbiology into economic analysis enables the development of more comprehensive and interdisciplinary approaches to studying economic systems. This intellectual cross-pollination enriches economic theory, providing valuable perspectives for addressing contemporary economic challenges and designing more effective policies and strategies. Through this lens, economists can better understand and predict complex economic behaviors, enhance resource allocation efficiency, and foster sustainable development.

Marshall's vision highlights the importance of viewing economic systems through the dynamic and adaptive processes observed in biology. This perspective not only broadens the scope of economic research but also fosters a deeper understanding of the complexities inherent in economic systems, ultimately leading to more robust models and innovative solutions for real-world economic challenges.

Conclusion: the complexity of interdisciplinary analysis—beyond simplified concepts in economics and microbial studies

The integration of ideas across diverse fields of research sparks fresh perspectives, paving the way for novel insights and innovative problem-solving approaches. As a source of inspiration for future interdisciplinary studies on microbial communities, this paper advocates applying BMT to provide a robust framework for understanding and explaining the various cooperative interactions facilitated by microbes. By extending the concept of market economy, this paper sheds light on socio-microbiology.

A prime example of this interdisciplinary application is seen in the realm of metabolic exchange among microorganisms. Metabolic exchange serves as a fundamental process in which microorganisms engage in mutually beneficial resource sharing to promote their individual growth. This phenomenon is prevalent in microbial communities and plays a pivotal role in a complex web of cooperative interactions throughout the biosphere. Microbes exchange various metabolites, such as essential amino acids, sugars, fatty acids, and cofactors, influencing the dynamics, stability, and evolution of microbial networks. For instance, in a microbial consortium, one microbe might produce a vital nutrient that another microbe requires for its growth, creating an interdependent relationship within the community. This paper extends the concept of market economy, traditionally applied in economics, to microbial ecosystems, illustrating how microorganisms engage in collaborative and competitive dynamics similar to human economic transactions.

In microbial populations, the exchange of metabolites resembles trade in an economic market. Microbes possess the capacity to convert various resources into forms that support their growth. They have mechanisms to transport metabolites between their intracellular compartments and the surrounding extracellular environment, which is rich in diverse metabolites produced by neighboring microbes with varying physiologies. In such an environment, there are opportunities for mutual resource exchange among microbes, analogous to how countries trade to enhance their material well-being.

Beyond metabolic trade, the significance of spatial positioning introduces another dimension of economic analogy. Spatial economics in microbial interactions draws from the market economy, focusing on the geographical concentration of trade. It shows that spatial positioning is crucial for both economic activities and microbial behaviors. Economic models that explain trade dynamics through factor endowments are similar to how spatial arrangements in microbial communities determine survival strategies. Strategies like biofilm formation and quorum sensing are essential for the resilience of these communities. They mirror urban economic principles, where being close together enhances productivity, much like the innovation ecosystem in Silicon Valley. Biofilms in microbial life serve as examples of how structured environments are key to optimizing nutrient exchange and providing protection. This highlights the importance of spatial organization in boosting both the functionality and adaptability of economic and biological systems.

Moving deeper into economic parallels, the concept of comparative advantage offers further insight into microbial cooperation and specialization. Comparative advantage sheds light on the benefits of trade and specialization across both global economies and microbial ecosystems. This principle emphasizes the importance of tapping into areas of relative efficiency to enable exchanges that boost productivity and resilience. Mirroring this economic principle, microbial networks engage in metabolite trading and specialization, thus improving their collective well-being in ways similar to economic outsourcing. The Black Queen Hypothesis illustrates how microbial systems leverage comparative advantage, promoting a reductive evolutionary approach for the common good. This insight into microbial systems suggests potential biotechnological innovations, where utilizing the comparative advantage could lead to more efficient bioengineering practices and sustainable solutions.

Similarly, the exploration of altruism within microbial interactions reveals that some microbes perform roles benefiting their community at their cost. These altruistic actions in microbes mirror the CSR initiatives of companies within socio-economic frameworks. This behavior, manifested in the production of metabolites at the expense of their resources and energy, challenges traditional perspectives on microbial competition. It suggests that, under certain conditions, cooperative behaviors can become evolutionary stable, enhancing the resilience and collective fitness of microbial ecosystems. This evolutionary approach, devoid of conscious intent unlike human altruism, highlights the fundamental principle that such cooperative behaviors are driven by genetic advantages and survival benefits, contributing to the overall stability and diversity of the biological ecosystems.

While the fusion of economics and biological research is promising, it navigates through a complex landscape of interdisciplinary challenges. Bridging economic theory and biological research holds the promise of uncovering untapped insights, although it requires navigating the complex landscape of interdisciplinary study with precision and care. The shared terminologies between economics and biology, each bearing distinct meanings and implications within their respective disciplines, demand careful interpretation to avoid misrepresentations. Moreover, the anthropomorphic application of economic behaviors to microbial actions can oversimplify the complex mechanisms governing microbial communities. Navigating these challenges necessitates an explicit understanding of the terminologies and foundational assumptions unique to each field, steering clear of oversimplification and ensuring a more accurate interdisciplinary dialogue.

Applying economic principles in biology or vice versa can deliver new impetus in the research of each field as well. The convergence of economic principles and biological research enhances the understanding of microbial ecosystems and paves the way for groundbreaking collaborations between economists and biologists. This interchange of ideas has the potential to reshape problem-solving approaches in both domains. However, to facilitate these collaborations, a thorough analysis of how economic problems, with all their assumptions, can be translated into a biological setting is imperative. This work is the first attempt to define a dictionary allowing such translations, and thereby easing communication. In summary, these findings prompt a fresh perspective on socio-economics in microbial biology, urging researchers to actively engage in interdisciplinary dialogues. These discussions, involving experts from diverse fields, encourage the exploration of thought-provoking questions, the pursuit of new avenues and methods, and the shared learning from each other's distinct scientific experiences.

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Data availability

There is no additional data.

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