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# The dawn of ethnomicrobiology: an interdisciplinary research field on interactions between humans and microorganisms

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### **Abstract**

**Background** Ethnobiologists commonly analyze local knowledge systems related to plants, animals, fungi, and ecosystems. However, microbes (bacteria, yeasts, molds, viruses, and other organisms), often considered invisible in their interactions with humans, are often neglected. Microorganisms were the earliest life forms on Earth, and humans have interacted with them throughout history. Over time, humans have accumulated ecological knowledge about microbes through attributes such as smell, taste, and texture that guide the management of contexts in which microorganisms evolve. These human-microbe interactions are, in fact, expressions of biocultural diversity. Thus, we propose that ethnomicrobiology is a distinct interdisciplinary field within ethnobiology that examines the management practices and knowledge surrounding human-microbe interactions, along with the theoretical contributions that such an approach can offer.

**Methods** We reviewed scientific journals, books, and chapters exploring human-microbe relationships. Our search included databases such as Web of Science, Scopus, Google Scholar, and specific journal websites, using keywords related to ethnomicrobiology and ethnozymology. To categorize activities involving deliberate human-microbial interactions, we examined topics such as fermentation, pickling, food preservation, silaging, tanning, drying, salting, smoking, traditional medicine, folk medicine, agricultural practices, composting, and other related practices.

**Results** Our research identified important precedents for ethnomicrobiology through practical and theoretical insights into human-microbe interactions, particularly in their impact on health, soil, and food systems. We also found that these interactions contribute to biodiversity conservation and co-evolutionary processes. This emerging interdisciplinary field has implications for food ecology, public health, and the biocultural conservation of hidden microbial landscapes and communities. It is essential to explore the socioecological implications of the interwoven relationships between microbial communities and humans. Equally important is the promotion of the conservation and recovery of this vast biocultural diversity, along with sustainable management practices informed by local ecological knowledge.

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**Conclusion** Recognizing the dawn of ethnomicrobiology is essential as the field evolves from a descriptive to a more theoretical and integrative biological approach. We emphasize the critical role that traditional communities have played in conserving food, agriculture, and health systems. This emerging field highlights that the future of ethnobiological sciences will focus not on individual organisms or cultures, but on the symbiosis between microorganisms and humans that has shaped invisible but often complex biocultural landscapes.

Keywords Ethnobiology, Microbiology, Traditional ecological knowledge, Sustainability, Social justice

### **Background**

Ethnobiology is a field of research that encompasses complex bodies of knowledge, cosmologies, actions, and interactions between people and biodiversity, operating at the intersection of several scientific disciplines that address both cultural and biological issues. It therefore involves the study of highly diverse, dynamic, and historical relationships between people, biota, and environments [1-3]. To date, much of this research has focused on terrestrial vascular plants, macromycetes, vertebrates, and insects. However, there is increasing interest in traditional knowledge related to other taxonomic groups that contribute to biodiversity and their interactions with cultural diversity [4, 5]. One of the central goals of ethnobiology is to integrate knowledge systems from diverse stakeholders, which is especially relevant when addressing socioecological challenges [6]. As a result, this interdisciplinary approach has evolved through different epistemological frameworks and historical stages [2–6].

Ethnobiology has been shaped by diverse biological perspectives, with integrative strategies related to knowledge systems varying across cultures worldwide [7–10]. Historically, attempts to explore the complex relationship between biodiversity and cultural practices have often focused on specific taxonomic groups. Ethnobotany, for example, focuses on human-plant interactions [7, 11, 12], while ethnozoology focuses on human-animal relationships [13–17]. Although less studied, organisms such as fungi (especially macro fungi) have also been studied by ethnomycology, which examines their role in food, medicine, recreation, and household economies [18, 19].

In contrast, the relationship between humans and the microbial world has received relatively little theoretical attention, even though microorganisms are the earliest and most diverse organisms on the planet. Microbes play a critical role in human food and health systems, and their activities and byproducts are often experienced through smell, taste, texture or other attributes. Throughout Earth's history and the development of civilizations, a complex, multilateral relationship has developed between humans, the environment, and microbial communities [20]. Despite their vast diversity,

microbes have been largely overlooked in ethnobiological studies, even though they are integral to the ecological interactions that many ethnobiologists study.

The term "ethnomicrobiology" is rarely used in scientific literature, and evolutionary ethnomicrobiology has yet to be formally established. The term was first introduced by Souza [21] in a study of traditional agricultural practices in Mexico, where local people from Puebla and Morelos managed Phaseolus species and their associated Rhizobium bacteria. These authors found that farmers were aware of how their practices positively affected soil microbial communities and crop yield, drawing attention to an often-overlooked aspect of ethnobiology. Subsequently, Tamang [22-24] defined ethnomicrobiology as a field focused on understanding the indigenous knowledge used to produce culturally and organoleptically acceptable fermented foods through natural fermentation. However, this definition may be too narrow, given the wide range of processes involving human-microbial interactions. Other authors have proposed the term "ethnozymology" to describe the science of fermentation in traditional diets, emphasizing the integration of Traditional Ecological Knowledge (TEK) into fermentation practices, using native, autochthonous microbiota from plant ingredients and other natural sources [25]. This approach highlights the role of TEK in guiding the dynamics of microbial communities associated with fermented products. However, these concepts may be limited when considering the full range of human-microbe interactions.

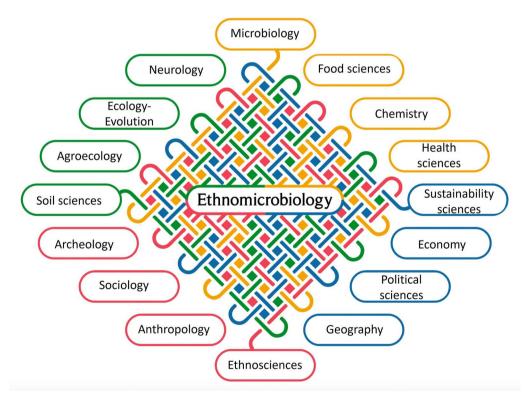
The primary goal of this work is to review the existing literature on the diverse range of human-microbe interactions, in order to establish ethnomicrobiology as a cohesive field that unifies concepts and develops theoretical and methodological frameworks for studying these relationships. We aim to contextualize the historical and dynamic interactions between microorganisms—whether at the level of population, community, species, or strain levels—and human activities. As an interdisciplinary and transdisciplinary field, ethnomicrobiology incorporates multiple theoretical and methodological perspectives to study the relationships between microorganisms (including

bacteria, viruses, fungi, and archaea) and human cultures (Fig. 1). We recognize the critical role that microorganisms have played throughout human history and their ongoing influence in areas such as food, health, and various production systems. This approach provides ethnobiologists with valuable research tools to analyze how different cultures perceive and interact with microorganisms, how microbial communities are conserved, maintained, and utilized in different contexts, and how these interactions shape the interplay between the micro and macro worlds.

Ethnomicrobiology is based on the ethnobiological goal of understanding and reflecting on local knowledge about microorganisms and the products that result from these interactions. The emerging ethnomicrobiological framework seeks to recognize and value the skilled individuals who manage the invisible microbial world, whom we will refer to as microbial managers. It also seeks to move beyond stereotypes that frame indigenous peoples' knowledge of biotic relationships as primarily visual and to open

new ways of exploring biodiversity through other senses

In this work, we explore the global developments and trends in ethnomicrobiology. This review offers a novel and original perspective that addresses the emerging growth of this field within the ethnosciences and its future directions. We conducted a systematic review of scientific journals, books, and book chapters that address human practices or traditional knowledge in the management of microbial communities in soil, fermentation, and health. We include peer-reviewed works of qualitative and quantitative research, reviews, and dissertations. We also include studies from the last 30 years, unless older studies are foundational or critical for the review. We limit our search to studies published in languages not covered by the research team's language skills, opinion pieces, letters to the editor, or non-peerreviewed articles. Our search included articles from international databases such as Web of Science, Scopus, Google Scholar, PubMed, and specific journal websites. We focused on terms related to ethnomicrobiology,



**Fig. 1** Ethnomicrobiology is an interdisciplinary and transdisciplinary field that bridges ethnobiological studies (red color below) and microbiological sciences (yellow color above). Rather than being treated as an independent branch of ethnobiology, ethnomicrobiology requires the collaboration of various biological and social sciences to unravel the complex and intricate effects of human-microbial interactions (all the colors in between the coalition of major disciplines). We envision ethnomicrobiology as a vibrant, woven textile, where different disciplines intertwine to propose a unified concept and diverse perspectives on human-microbe interactions across ecological, cultural, economic, functional, evolutionary, chemical, and other approaches. This emerging field and all the perspectives involved allow us to rethink the historical and dynamic relationships between microorganisms and human activities in a myriad of ways (Image by Alejandra Cruz Rodriguez)

ethnozymology, fermentation, traditional knowledge, microbial management, fermentation and cultural practices, and microbes.

In this review, we emphasize the implication of ethnomicrobiology in shaping both microbiological and ethnobiological research agendas. The following sections explore a wide range of activities that involve intentional human-microbial interactions, including practices designed to preserve, promote, maintain, or eliminate microbial groups. These practices encompass food preservation techniques such as fermentation, pickling, drying, salting, and smoking, as well as practices intended to avoid microbes, such as tanning. In addition, we will examine microbial management activities in soil, including agricultural practices, composting, and geophagy. We also discuss the role of microorganisms in traditional and folk medicine, where microbial management is integral. In addition, we highlight the relevance of ethnomicrobiology to evolutionary studies, particularly by integrating microbial research trends with evolutionary frameworks such as the domestication of microbial fermentation environments, niche construction, and the co-evolution of microbes with domesticated plants. Finally, we address the socialcritical dimensions of ethnomicrobiology, emphasizing its importance for understanding broader societal and ecological dynamics.

# The relevance of ethnomicrobiology to the microbiological and ethnobiological research agenda

Do humans have microbial blindness, or do we rely on visual cues to the detriment of our other sensory data collection? Certainly, we live in a microbial-dependent world; without microbes, important geochemical cycles such as those of nitrogen, carbon, and phosphorus would collapse, decomposition would stop, and no animal (including humans) would be able to produce and digest its food, and life as we know it would truly cease to exist [26]. It is common for many people to associate microorganisms with agents that cause diseases in plants and animals. However, throughout history, humans have used microorganisms for a wide range of activities. Our relationship with these diverse organisms is both intimate and vital, affecting various aspects of our daily lives, including functions of which we are often unaware [27-29]. The formal study of microbial communities only began after technological advances in microscopy and the pioneering work of scientists such as Koch, Pasteur, and De Bary in the late nineteenth century. These advances stimulated interest in microbiology as a scientific discipline. However, long before microbes were understood, human cultures around the world engaged in activities such as salting, smoking, roasting, lyophilization, nixtamalization, tanning, and fermentation of foods, beverages, and dyes, all of which involved microbial management processes [30–37].

Microbiology is the study of microscopic organisms, including unicellular, multicellular, or acellular forms [38, 39]. It includes both eukaryotes, such as fungi and protists, as well as prokaryotes, viruses, and prions. Although prions and viruses are not considered living organisms in the strict sense, they are part of the microbiological agenda. Microbiology also serves as an umbrella for several subfields, including virology, mycology, parasitology, bacteriology, immunology, and zymology, all of which study different aspects of microorganisms. The interactions between humans and the microbial world have revolutionized life, particularly in medicine through the use of antibiotics, and vaccines, reducing the incidence of infectious diseases [40, 41] (in Fig. 1, related disciplines of microbiology shown in yellow). Microbiology has also made significant contributions to fields as environmental such management, genetics, and molecular biology (in Fig. 1, related disciplines of microbiology shown in green), but perhaps its most profound impact has been in food production and biotechnology, evident in the wide range of products such as wine, bread, and cheese, among others [42-44].

Despite significant advances in microbiology, the vast empirical knowledge of microbial processes held by traditional societies has often been overlooked. Microbes have been understood and managed in all human cultures for centuries [45]. Many communities engage in agricultural and culinary practices that directly shape microbial communities in both soil and food [46, 47]. The diversity of fermented foods resulting from these practices is critical not only for human nutrition but also as a form of cultural expression [48]. Moreover, these interactions extend beyond food, encompassing traditional health practices, which often involve microbial activities [48]. A deeper understanding of local knowledge systems related to microbial management may reveal microorganisms as an integral part of local biodiversity with significant health benefits.

One approach often used by ethnobiologists is the biocultural perspective. If we consider biodiversity to include the vast diversity of microorganisms, it becomes crucial to recognize these microorganisms as agents that establish relationships with human groups and cultures. Integrating these biological entities into ethnobiology has significant implications, especially since human interactions typically involve entire microbial communities, populations, strains, or even entire microbial ecosystems, rather than just individual species. While there are prominent examples

of interactions with specific microorganisms, such as those used in beer production or the use of *Aspergillus* in cheese-making, these relationships often reflect broader ecological dynamics that involve multiple senses and extend beyond mere visual perception. Understanding our relationships with microorganisms requires attention to these multisensory interactions. In addition, the management and production of artifacts to manipulate microbial groups play a critical role in this complex web of interactions between living organisms, objects, and humans [49].

Incorporating microbiology into ethnobiology is critical for understanding ecological knowledge, cultural meanings, and the sustainable management of microbial biodiversity. It also provides insights into how human actions shape microbial communities and influence selection or domestication processes that favor certain microbial groups over others. In addition, studying the effects of human management on plant and animal microbiomes highlights the interconnectedness macroorganisms and microorganisms. Ethnomicrobiology also opens discussions on ethical issues such as the use of microorganisms, bioprospecting, biopiracy, and intellectual property rights. Moreover, it serves as a reminder that we live in the "Microbiocene", an era in which we must acknowledge our dependence on these organisms, even if we often experience them primarily through their "osmocosm" (the scents of the universe) [50].

# Identifying activities that involve deliberate actions on human-microbial interactions

Historically, ethnobiological studies of plants and animals have explored a wide range of topics, including behavior, use, cultural transitions, social relationships, and their ecological and evolutionary implications [7, 51]. Plant and fungus collectors, managers, and domesticators possess extensive knowledge of the taxonomy, biology, and ecology of these species, just as hunters, ranchers, and breeders do for animal groups [17]. Local experts play a critical role in preserving and transmitting ecological knowledge about human interactions with biota [52, 53]. Similarly, people around the world engage in a variety of practices to manage microbial communities. Whether to maintain, promote, restrict, or eliminate them, these human practices represent diverse forms of microbial management (Fig. 2). Today, different cultures have different relationships with microorganisms, which we will outline in the following section.



**Fig. 2** Activities that involve microbial management. Fermentation is a universal process used to produce foods, beverages, dyes, and other products. In these processes, specific microbes are managed and selected to produce desired products, while other microorganisms that may cause spoilage are intentionally avoided. Preservation practices involve physical methods such as drying, smoking, salting, and tanning to restrict microbial communities that could lead to spoilage. Soil management practices are widely used around the world, to encourage beneficial microbes that improve soil health and ultimately agricultural yields. On the health front, many diseases are linked to imbalances in the microbial communities within the human body. Folk and traditional medicine has long employed practices to maintain balance within these communities. In addition, the increase in health concerns in recent years has highlighted the importance of a healthy diet, particularly the consumption of fermented products, in maintaining microbial balance. (Images created using Copilot in Windows AI)

### Fermentation for food and beverages

Fermentation is perhaps the most tangible and oldest technique that allows humans to perceive and interact with the microbial world in their daily lives, even without seeing the agents responsible for this transformation. Fermentation is a metabolic process carried out by various organisms to produce energy. Microbial groups such as bacteria and yeasts convert organic compounds such as carbohydrates through enzymatic reactions (mainly in the absence of oxygen) into simpler molecules such as alcohol or a wide variety of organic acids [54, 55]. Fermentation has been used as a common process in the production, preservation, enhancement, and transformation of various foods and beverages [54, 55]. However, other products such as textiles, dyes, compost, and many other common commodities undergo fermentation processes [56, 57]. In the food industry, fermentation has facilitated the increasing production and diversification of foods and beverages; in fact, it is estimated that approximately an average of 50-400 g per capita of fermented foods and alcoholic beverages are consumed daily worldwide, accounting for approximately 5–40% of the total daily food intake by humans worldwide [58-61]. These products are not only essential to the human diet but have also played a historically significant role in shaping the socio-economic, cultural, and identity aspects of human life [59, 62-64]. Thus, these products should not be considered as commodities alone, but as part of the complex cultural contexts in which they are embedded.

Microbiological studies have generally assumed that traditional fermentations capture wild and mostly uncontrolled organisms, resulting in heterogeneous unpredictable outcomes for biotechnological purposes or even products that may endanger human health [65]. However, several studies have documented complex knowledge systems by which people manage the effects of such heterogeneity through practices such as controlling the room temperature, covering the fermentation containers, adding specific plants that contain enzymes for food fermentation processes, or as other sources of more specific microbial communities [66-68]. In addition, some producers have conditioned or constructed specific fermentation rooms, containers, and other facilities that play an important role in promoting the collection of microbial communities and other practices that help maintain them by avoiding cleaning chemicals and soap [69, 70].

Fermentation can be accomplished using inoculants, also known as starters or starter cultures, which are established microbial consortia added to initiate, enhance, or drive the fermentation process [71–75]. Similarly, backslopping is the practice of using a

portion of a previous batch of fermented food or beverage to inoculate a new batch. This is commonly done in processes such as sourdough bread making or yogurt production [76, 77]. The purpose is to inoculate an old batch to start the fermentation process with new substrates by introducing those beneficial microorganisms from a previous batch [71, 76]. All these techniques of fermentation represent strategies to gather microbial communities, but in between, several practices are performed by producers to obtain accepted fermented products. However, the cues or motives to use one or another are a topic to be studied in numerous contexts to obtain signals of possible trends in the management of microorganisms or to understand that practices are unique to each cultural group/microbial manager or fermented product [61].

Fermentation introduces what we call "gastronomic plasticity," which refers to the ability of a culinary tradition to adapt, evolve, and incorporate new ingredients and techniques. This flexibility allows the tradition to respond to dynamic changes in resource availability, cultural exchange, and consumer preferences by expanding the range of flavors, textures, smells, aromas, and other qualities in the final product. However, how people "collect sensory attributes" and how they manage contexts that influence the invisible world to achieve the desired properties is a major challenge to study within an ethnomicrobiological framework.

This could be a complex issue as the answers could be variable depending on the region, the environment, the products, the human culture, and the producers and the practices used. Nevertheless, there is a remarkable ability of producers to recognize and remember or even name certain smells, tastes, colors, and textures of fermented products by the producers. For example, indigenous microbial managers identify the same flavor, texture, and aroma resulting from the presence of endophytic bacteria, such as Leuconostoc mesenteroides, in aguamiel, pulque, comiteco, and certain types of mezcal from the Mexican Altiplano as they do in Agave salmiana Otto ex Salm-Dyck spirits [78]; this may be due to the common use of pulque and its associated microbial communities as starter cultures for other fermented products [62]. This idea has been proposed by several authors who seek to identify a "microbiology of desire" through which some microbial consortia could be selected for their specific organoleptic profile [79].

There are outstanding studies that address this idea by following the changes in the microbial communities, the odor in the successional process of fermentation, and the functionality of the microbial groups [80–83]. There are some clues as to how the microbial community affects the final attribute of the fermented product; however,

no information has been reported on the clues that producers recognize when the fermentation needs to be controlled.

To address these complex bodies of knowledge and practices, the ethnomicrobiological approach can be used to identify techniques that managers apply to achieve specific sensory attributes in their fermented products. It can be used to understand the choice of containers or how they design the facilities to carry out the fermentation. Also, different information can be obtained through ethnographic studies of flavors and how they categorize the different flavors, odors, and textures, but also this can be contrasted with techniques such as Solid-Phase Micro-Extraction (SPME)-Gas Chromatography/ Mass Spectroscopy (GC/MS), which has been widely used to qualitatively and quantitatively determine the volatile compounds responsible for aroma and flavor. It should also be accompanied by the characterization of the microbial community present in the product. In this sense, the interdisciplinary combination of different approaches and types of information, such as qualitative and quantitative, could bring theoretical and practical insights crucial to identify the selection and domestication process of microbial communities and specific strains and mechanisms to guarantee the viability of this microbial world.

### Retting: yarning of fermented fibers

Fermentation is also a fundamental process for organic materials and has been used as a practical technique to process and obtain specific quality fibers. Retting is used to describe the soaking or wetting of flax, hemp, or other stalked fiber plants, as well as "coir" fibers from coconut shells, cassava tubers, and other fibrous plant materials [84]. Retting generally begins as a spontaneous fermentation that digests pectin and other compounds, thereby releasing the fibers and making them available for further applications such as rope, yarn, paper, and many other products [84]. In countries such as Mexico, the production of fibers by fermentation is a traditional practice that has been documented but remains relatively understudied. For example, fibers are produced by fermentation of the inner bark of the jonote tree (Heliocarpus appendiculatus). Although this practice is now largely abandoned, it remains important in certain regions in the southern region of Mexico, particularly in the Sierra Norte de Puebla by the Nahua and Otomi ethnic groups, and in Veracruz, where it is still practiced by the Totonac groups [85-87]. The characterization of the production practices has not been finely detailed and less is known about the microbial community, nor the cues that producers recognize to obtain the optimal quality of the fibers. However, the general process aims to remove the slime through a long fermentation process of eight days, then producers start to obtain fibers that are resistant and have a long durability [85–87].

### Dyes: coloring by fermentation

Before industrialization and the development of synthetic dyes, many tinctures were traditionally derived from plants and minerals. Today, many of the natural dyeproducing plants and practices are still struggling against cultural homogenization and shifting to industrial dyes [88, 89]. It is astonishing how many plants and practices have been poorly recorded and lost just for dye production. Historically, one of the most popular herbaceous plants used for dye production is woad (*Isatis tinctoria* L.), which is used in Asia and Europe for traditional cloth dyeing through the extraction of indigo [90–93], while in other regions such as Peru, Mexico, Central America, the Philippines, and Indonesia the production of indigo pigment is mainly obtained from *Indigofera suffruticosa*.

Traditionally, indigo is produced by harvesting the leaves and grinding them in mills to produce a dense paste, which is then fermented [94, 95]. Fermentation practices for indigo production vary from region to region. In European locations, fermentation typically lasts 10 to 15 days, with variations depending on temperature and other factors. In other cases, the water is replaced with a mixture of water and urine, lime, or wine [94, 95]. Although these plants were important in the production of dyes, the knowledge of how to make them was almost lost. Today an increasing demand for natural dyes has raised awareness of the need to maintain the production of these pigments using traditional methods [96–98]. Fermentation is a delicate part of the indigo reduction process [92]. Several practices are used to control indigo reduction, the most common being maintaining the fermentation temperature, but also, the use of alkaline agents such as wood ash, slaked lime, or potash [94]. At this stage, it is possible to obtain different hues by using different proportions of these components [94].

Color is important in human social and religious life, as part of clothing, ornaments, art, food, and drink; the pigments of animal, vegetable, and mineral origin are all valuable resources. In Mexico, for example, knowledge of the coloring properties of plant parts such as roots stems, leaves, flowers, and fruits [99], and animals such as cochineal (*Dactylopius coccus*) and the purple snail (*Plicopurpura pansa*) was vast and is being lost with time. In Mexico, 541 plant species have been registered for artisanal use, of which at least 90 have been registered for dyeing applications [100–102]. For example, the production of indigo in some Mexican localities requires

specific practices to obtain darker shades of blue. To achieve this, the producers carry out a controlled fermentation process in clay jugs that lasts 3 to 6 months. The powdered indigo is then mixed with water, rotten agave leaves (*Agave atrovirens*), and urine from women or babies who have been fed with a special diet in the preceding days [103]. After proper fermentation, the dye is obtained and ready for use. Wool or cotton is dipped into the wort and may be dyed several times to achieve the desired shade [102, 103].

Such a delicate and complex process was mainly carried out by the specialized dyers in a completely empirical way, which became the "secrets" of each master, the color, the smell, and even the taste of the bath liquid was, for a long time, the only elements that the dyer could use to control the fermentation and dissolution processes [104, 105]. This specialized knowledge can be followed by an ethnomicrobiological approach to fill gaps or gain insight into the differences in microbial communities, depending on the fermentation practices. Although several studies have been conducted to characterize the microbial composition in dye vats around the world [102-105], few studies have addressed the importance of integrating ecological knowledge for optimal dye production and the changes in microbial communities [106–108]. Documenting such knowledge is critical to meet the growing demand for natural dyes in textile dyeing operations, which is increasing due to the manufacturers' awareness of the toxicological data of the materials, the wear of the dyed fabrics, and the effluents generated by dyeing industries [109].

### Silage

Ensiling is a widely practiced method of preserving and fermenting green forage from crops and non-crop plants such as weeds and wild grasses, to produce silage, a highquality feed for livestock, particularly during periods when fresh pasture is unavailable [110-112]. The process of silage production varies across regions, depending on factors such as plant species, livestock species, and local practices. In general, the process begins with harvesting the crop at its optimal stage of maturity, when it is not too ripe, to ensure the highest nutritional value and ideal moisture content for fermentation [110–112]. After harvesting, the forage is chopped to increase sugar availability, which optimizes the fermentation process [113-115]. The chopped forage is then stored using various techniques, most commonly in silos or pits, but traditional methods are also employed to remove air from the forage mass [113–115]. Once compacted, it is crucial to create an airtight environment to facilitate fermentation. Effective sealing methods include the use of plastic sheeting, tires, or specially designed covers, all aimed at maintaining the anaerobic conditions necessary for fermentation [115].

Fermentation is primarily driven by lactic acid bacteria (LAB) that are naturally present in the plant material or introduced as inoculants. These bacteria acidify the substrate and inhibit the growth of spoilage organisms such as enterobacteria, clostridia, yeasts, and molds. The ensiling process is influenced by several cultural practices and ecological knowledge that vary according to environmental factors [116–118]. However, many of these practices remain undocumented.

We propose that an ethnomicrobiological framework could provide valuable insights for diversifying and improving ensiling techniques, as well as for managing the microbial diversity associated with silage production. This approach could also provide theoretical contributions to practices involving the selection or domestication of microbial communities related to these products.

# Food preservation strategies: microbial management for food security

Since early history, humans have needed to store and preserve food. For example, the ancient Semitic term mouneh, found in languages such as Arabic, is derived from the primary lexeme "mana," which means to store or preserve for future use. Pre-Biblical Middle Eastern traditions of food preservation included lactic acid fermentation of kefir rubbed into grains, pickling in vinegar, wine, and bitters, and the use of infusions and acidic citrus juices. These traditions also included curing meats and fermenting cheeses, yogurts, kefirs, fruits, and roots throughout the Levant. In Lebanon alone, tens of thousands of Christians, Muslim, and Druze women continue to engage in the seasonal preparation of mouneh to ensure food security in times of crisis, whether due to war, government instability, locust plagues, drought, or other climatic disasters [119].

Throughout history, the inquisitive human mind has continually innovated and discovered various food preservation systems that have influenced numerous cultures over time [120]. These preservation techniques have allowed humans to store food for later use, rather than consuming it immediately after killing or harvesting [120]. Early human preservation practices were primarily based on daily experience, and many traditional methods in developing countries still adhere to this approach [119, 120]. Today, there is an increasing demand for fresh foods that retain their natural nutritional value and sensory attributes, such as flavor, odor, texture, and taste. This shift has created challenges for food technologists who are tasked with developing safe, minimally processed foods with minimal or no synthetic additives [121–123].

Although creating such foods with an adequate shelflife is complex, traditional microbial managers have long developed practices to minimize microbial contamination in foods, beverages, and other products. These techniques vary widely in different regions of the world and involve actions that either prevent the growth of spoilage-associated microbes or limit microbial activity as much as possible. This is particularly important as foodborne illness is still prevalent in many regions. In addition, microbial management practices often promote beneficial microbes for their positive effects on sensory attributes. As a result, these techniques focus on controlling or inhibiting specific microorganisms or the whole microbial community, while fermentation is used to promote the growth of beneficial microbes and inhibit those associated with spoilage.

### **Drying**

Drying is an ancient food preservation technique used in the direct preparation of food products and further processing in various applications in food and non-edible products. Typically, drying is used to convert a surplus crop into a shelf-stable commodity. It has always been valuable to ensure the availability of food and medicine throughout the year. Drying used to be natural and simple because the process was driven by solar energy, but recently several technologies have emerged to speed up the process [124–126]. Drying preserves the product and can affect the quality of materials such as spices, medicinal plants, herbs, and bioactive enzymes, that can generate value-added compounds during drying [125-127]. Drying is the process of unbound moisture removal, followed by internal moisture elimination [127]. Removal of moisture prevents microbial growth [127–130].

Freeze-drying is a method of removing water from frozen material by sublimation of ice crystals [131, 132]. Although this practice is limited to cold regions, it is a traditional strategy for preserving various foods. For example, in Peru, specific techniques of freezedrying potatoes (Solanum tuberosum, S. juzepczukii, S. curtillobum) are performed to obtain white or black chuño. Chuño is produced mainly from larger bitter potatoes grown outdoors and subjected to this treatment for several days until managers recognize attributes such as a dry sound, or a texture like stones [133, 134]. Chuño producers also collect potatoes after freezing at night because sunlight causes the chuño to blacken and lose its most valuable characteristic, its white color [135]. After freeze-drying, the potatoes are trampled with bare feet to loosen the skin and remove as much liquid as possible [133, 134]. The potatoes are then left to dry in the sun for several days, which also limits microbial growth [136]. The main microorganisms involved in *chuño* potatoes are *Lactobacillus* species (*L. sakei*, *L. casei*, *L. farciminis*, *L. brevis*, *L. fermentum*) and *Leuconostoc mesenteroides* once *chuño* is stored. It can be transformed into *tocosh* (a fermented potato), and it develops several anti-bacterial properties [137].

### Smoking and roasting

Smoked and roasted foods have played an important role in the human diet and are still widely consumed and locally produced in different regions of the world. Smoking and roasting are among the oldest technological processes used by humans to preserve and enhance food [138]. Roasting is a food processing technique that uses heat to cook various products evenly, improving their digestibility, palatability, and sensory aspects, such as the development of color, aroma, flavor, phytonutrients, and antioxidants in foods and beverages [138, 139]. It also enhances the bioavailability of components through physicochemical and structural modifications of various food matrices [140]. The process can cook, gelatinize, expand, pop, or puff food materials, making them more accessible, appetizing, and attractive. In addition, heating aims to eliminate or reduce microbial load, natural toxins, and enzyme inhibitors. Roasting modifies the low-water activity in foods, which limits the growth of microbial communities, though several factors, such as unsanitary drying or storage conditions, contaminated equipment or managerial practices, and failure to control foodborne pathogens can still pose risks [141, 142].

Smoking food produces a suspension of solid particles in a gaseous phase consisting of air, carbon monoxide, carbon dioxide, water vapor, methane, and other gases, forming an aerosol [137]. During the drying process, the water activity of the food decreases, and components such as thymol, formaldehyde, formic, acetic, and benzoic acids, as well as orthocresol, metacresol, paracresol, guaiacol, methylguaiacol, cresol, and xinelone, contribute to bactericidal, antimicrobial, biocidal, fungicidal, and preservative effects [137, 143, 144], thereby limiting the growth of spoilage and pathogenic microorganisms. Several studies provide evidence of how microbial communities change during smoking [137, 143, 144]. Smoking remains a widely used technique for food preservation worldwide [145–148], with various smoked foods such as smoked meat, fish, seafood, cheese, beverages, spices, and flavorings being traditionally produced and still widely used [137, 149]. However, practices and processes vary from region to region.

In many traditional cases, smoked products are hung on shelves placed above where the smoke passes, and the smoke may result from the thermal decomposition of wood, although other biological sources such as coconut shells, corn ears, and even paper have also been used [137, 149, 150]. More recently, smoking as a preservation method has been replaced by modern techniques, such as controlled ovens and liquid smoke [146]. For many of these products, the cues that managers use to ensure a safe smoked product remain unclear, and characterization of the microbial community has, to our knowledge, only been addressed once [146]. Nevertheless, this may be an interesting topic to explore using an ethnomicrobiological approach.

### **Pickling**

Pickling is an ancient method of preserving various foods, dating back to at least 2400 BP, including vegetables, fruits, fish, and meat [151], using brine and/or vinegar. Pickling not only extends the shelf life of foods, but also imparts unique and desirable changes in flavor, texture, and color over time. This method has been an integral part of many human communities and cultures around the world. Pickling has deep roots in several civilizations [152], and the knowledge has traditionally been passed down orally [153, 154]. The main purpose of pickling is to preserve food by promoting an acidic environment, typically using enriched solutions such as vinegar, that control or halt microbial growth, while the food loses as much moisture as possible [151, 155]. In addition, brine pickling, in which the preservation is due to salt rather than fermentation, helps to develop different flavors and textures in the pickles [151]. From an ethnomicrobiological perspective, it is important to document how producers control the raw materials, microbial ecosystems, and fermentation processes, and to document the use of starter cultures that may be useful for promoting an acidic environment [156] and for producing other metabolites with desirable properties such as heterogeneous aroma compounds, bacteriocins, and exopolysaccharides [157], or with beneficial health effects [158-160].

These traditional methods mentioned above are crucial not only for extending the availability of food but also for improving its final quality and providing greater resilience to fluctuations in access. As the world's population continues to grow, so does the demand for food; however, food loss and waste occur throughout the entire food value chain, from production to handling, transportation, storage, distribution, and consumption [159, 160]. Therefore, these traditional practices are essential for preventing food waste. From an ethnomicrobiological perspective, all of these techniques are essential for supporting local food knowledge systems, which are intimately linked to survival and food sovereignty.

### Tanning as a leather sourcing practice

Leather tanning is an ancient practice in human technological history, involving the processing of hides and skins to produce various products [161], including clothing, footwear, handbags, musical instruments, shelter, and upholstery materials, among others [161]. This process made it possible to use tougher and more durable animal skins for clothing, and before the rise of the paper industry, many manuscripts were written on parchment [162]. From the eighteenth century to the late nineteenth century, the term "preservative" was commonly used by naturalists to describe tanning agents that preserved hides by preventing degradation by insects and microbes, thus producing antiseptic substances with preservative properties [163].

Today, various methods of skinning and preserving vertebrate skins have evolved, with taxidermy playing an important role [164]. The primary goal of tanning is to preserve the skin and prevent its deterioration after removal. This is achieved by reducing the water content and maintaining sufficiently stable collagen fibers using chemical compounds [165, 166]. Without this process, microbial communities would break down the skin, leading to decomposition, bad odors, loss of stiffness, and deterioration of the hide [165, 166].

Traditionally, the simplest way to prevent deterioration was through dehydration, achieved by ventilation, sun drying, or saline solutions. This was followed by a series of chemical and physical processes, including the removal of hide, cartilage, and fat. During this process, proteins were hydrolyzed before the addition of preservatives, which were applied in various forms such as powders, soaps, pastes, liquid infusions, and baths. These preservatives were primarily salts, minerals such as alum, and chromium, known for their oxidizing properties [167, 168]. Plant materials were also selected for their astringent properties, strong odors, and high concentrations of tannins [167, 169]. The term "tannins" is derived from the Latin word tannum, meaning "crushed oak bark" [170]. While tannins are best known for roasted powdered oak bark, other species, such as those from the genera Acacia, Caesalpinea, and Lysiloma of the Fabaceae family, are also used [171, 172].

Ethnobotanical studies have extensively documented the plant materials used to preserve leather. These studies have revealed various recipes, including mixtures of herbs (rosemary, thyme, laurel, bay, mint), peels (orange, lemon), and seeds (cumin, anise, cinnamon, pepper). In recent years, the use of plants with antimicrobial properties, such as *Moringa oleifera* and *Persicaria hydropiper*, has been effective in tanning goat hides, reducing salt and water contamination [173, 174]. Traditional leather tanning practices are primarily

passed down through oral and practical communication, resulting in gaps in the documentation of techniques used for different types of animal hides and the most common contaminants for each [170]. Some methods may have been lost due to a lack of recording, preservation, or publication. In addition, each producer often develops unique techniques that are constantly being innovated. It is important to recognize that most of these biotechnological applications are the result of ancient trial and error, and they should be acknowledged as part of historical development [171, 174].

### Soil: the managed microbial microcosm at our feet

Soil is one of our most precious resources on Earth. Down on the ground, constellations of microbes are responsible for imparting specific soil properties, and various researchers have focused their efforts on understanding and characterizing the "Earth's dark matter". Soil is one of the most complex and challenging environments for microbiologists because it contains the greatest microbial diversity on the planet, many of these microbes remain uncharacterized and represent a vast unexplored reservoir of genetic and metabolic diversity [175–178].

Soil plays a fundamental role in global ecology and agriculture. Several studies have shown that traditional soil management and crop selection promote a diverse soil microbial community due to crop heterogeneity [179]. To illustrate this idea the traditional farming system used in Mesoamerica, known as milpa, is an interesting example of soil microbial management [180-182]. The milpa system is characterized by the cultivation of several crops together in one plot, mainly maize, beans, and squash, thus promoting a symbiotic relationship, where beans provide nitrogen fixation due to an increasing number of active nodules per plant [183]. However, it is important to keep in mind that the composition of milpa system varies throughout Mesoamerica, so the number of microbial nodules varies depending on the plant species and varieties, but especially on the beans that are introduced into the milpa. Several ethnographic and microbiological studies have highlighted that different communities use practices such as the addition of local vegetation, and the promotion of weedy species, including medicinal plants or fruit trees, and microbiological studies have recorded that these practices promote greater genetic microbial diversity in the *milpa* soil than in wild sites or monocultures [184].

### Ethnopedology: soil knowledge by local people

Ethnopedology encompasses the soil and knowledge systems of rural populations, from the most traditional to the most modern communities [31, 185, 186]. Several studies within this framework have emphasized that indigenous communities classify soil attributes based on characteristics such as vegetation, color, texture, and other properties. Few studies have emphasized how different indigenous groups carried out a detailed characterization of soils, pointing out that they used these characteristics and practices for soil conservation, and to ensure the minimum loss of quality, fertility and other attributes [31, 185, 187]. Ethnopedology was proposed by Barrera-Bassols in 1983 [31, 185] as the science responsible for the study of the indigenous perception of the properties and processes of the soil, its nomenclature and taxonomy, its relationship with other ecological factors and phenomena, as well as its management in agriculture and its use in other productive activities [31, 185]. Ethnopedology emphasizes that indigenous classifications are based on knowledge accumulated over generations and are not only methodological but also based on theoretical knowledge constructed in a manner similar to that of formal science [31, 187, 188]. This knowledge is an essential resource for designing management strategies [189, 190]. Indigenous groups such as the Nahuas and Zoque of different municipalities in Veracruz, Mexico, identify soils of good quality for agriculture and pottery production but also soil used for geophagy. This type of soil is known as chogosta or xogos tall which is a "fermented" (bubbling) white soil used by the Nahuas to cure diseases related to the digestive system and will be addressed in the following section [190]. These types of soils have also been described in the detoxification of tubers in the Andean region [191].

In contrast, the modernization of agriculture has introduced external inputs such as industrialized fertilizers. Although the use of these inputs negatively affects soil microbial diversity [192–194], they are widely used by both small producers and large industries. In addition, a variety of hazardous pesticides (pure substances or chemical mixtures) are used by farmers in agricultural fields to control undesirable microbes during food production, harvest, and storage. These chemicals not only threaten crop fertility and productivity but also directly or indirectly affect human health [195]; most critically, they alter microbial diversity at multiple scales and systems.

Traditional management of agricultural and environmental systems is rooted in vast amounts of knowledge and beliefs, passed down through oral tradition and first-hand observation. Local knowledge about soil, health, and food is essential for decision-making in agriculture and natural resource management [196, 197]. For thousands of years, most societies have been predominantly agricultural, with daily interactions

between people and the land [198]. Through this continuous interaction, farmers have developed an intimate understanding of the condition, distribution, use, and care of the soil, the ecosystems in which they operate, and the relationship between these elements and their culture [31, 186, 189]. Evaluating traditional and ecological practices from an ethnomicrobiological perspective can provide practical applications for addressing global challenges such as food security, climate change mitigation, water security, biodiversity conservation, and ecosystem services [199, 200]. It offers practical insights into decisions regarding the use of fertilizers and pesticides, as well as strategies to reduce reliance on external industrialized inputs that compromise microbial diversity, health, and economic well-being, ultimately striving for environmental, health, and biological integrity.

### Composting

Composting is another important microbial management practice. It is a natural process that facilitates the decomposition and stabilization of organic matter in waste, allowing bacteria and fungi to transform organic materials by using carbon and nitrogen as energy sources, along with water and oxygen, to restore soil fertility [200-202]. A wide variety of composting practices and methods are used around the world, making it a crucial technology for recycling biodegradable waste into a useful product. Even without deliberate management, organic matter will naturally break down through microbial activity [84]. Composting systems vary from simple backyard piles and bins to highly sophisticated, computer-controlled, mechanized processes [203]. Depending on the composition of the waste, it may be composted directly or homogenized before undergoing secondary treatment. Producers can also choose between aerobic or anaerobic composting to achieve specific characteristics in the final humic substances for the soil.

While composting is primarily a wild fermentation process, inoculants are sometimes added to improve or guide the results, presumably to enhance the production of various enzymes and thereby accelerate waste decomposition [201, 203, 204]. The primary goal of composting is to raise the temperature to eliminate pathogens and make the resulting compost safer. The composting process involves a microbial succession: mesophilic bacteria and fungi first break down simple compounds such as sugars and amino acids, raising the temperature rapidly; then thermophiles break down more complex organic matter, such as cellulose, hemicellulose, and lignin. During this phase, the organic carbon content decreases due to the metabolic activities of thermotolerant microbes. Finally, the cooling phase

is characterized by reduced microbial activity and a decrease in temperature [201–205].

ethnomicrobiological perspective could significantly contribute to the documentation of practices, microbial groups, and their functional roles in the remediation and degradation of chemical pesticides. This perspective could also enhance healthy production systems, it can improve the sustainability of agricultural systems and help to conserve these often-overlooked resources. For example, during the COVID-19 public health emergency, producers of the Mexican fermented beverage pulque (made from fermented agave sap) began preparing soil fertilizers by composting dead agaves and organic matter, using pulque as a starter due to its rich yeast communities, which produced a bokashilike fertilizer, an adaptation to the reduced demand for pulque during the public health emergency crisis. Studies have shown that this compost is rich in carbon and nitrogen content [206, 207], and producers have observed improvements in soil quality and their crops.

# Clay-eaters: geophagy links healthy soils with human health

In a previous section, we discussed soil management and classification, highlighting practices such as geophagy that play an important role in human health in various communities around the world. Geophagy, the practice of eating soil or soil-like substances, is practiced for cultural, nutritional, or medicinal reasons, and is particularly common among pregnant women [191, 208, 209]. Despite its prevalence, geophagy is a complex phenomenon that reflects the intricate microbial-human interaction. It is nearly universal, transcultural, and multicausal, with roots in spiritual and religious beliefs, ceremonies, and nutritional needs. Some researchers suggest that geophagy is an adaptive behavior, either to alleviate nutrient deficiencies or to protect against ingested pathogens and toxins [209, 210]. Others argue that it is non-adaptive and occurs either to relieve hunger or as a side effect of nutrient deficiency [211]. Human geophagy is primarily explained as a protective measure against dietary chemicals, parasites, and pathogens. The benefits or harms of soil ingestion in humans are still debated, and little is known about the criteria consumers use to select soil for ingestion.

Among the beneficial aspects of clay consumption is the use of kaolin (a type of clay) in the treatment of diarrhea, gastritis, and colitis. It also allows the maintenance of normal intestinal flora with the help of commensal microorganisms found in the soil [212]. Kaolin is mainly consumed by women, during pregnancy, as a dietary supplement [213–215]. Beneficial microorganisms such as nitrogen-fixing *Rhizobium* spp. are associated with

these clays and may provide health benefits [216, 217]. Studies have reported that clay minerals could serve as inexpensive, highly effective antimicrobials for fighting various human bacterial infections, including those caused by *Mycobacterium ulcerans*, for which there are no effective antibiotics and mostly because some clays or soils contain specific components that act as valuable oral and topical antimicrobials and toxin adsorbents [218, 219].

Clay consumption can also be harmful due to its microbiological underpinnings, such as the ingestion of parasitic worm eggs (Ascaris lumbricoides, Trichuris trichiura), leading to significant health consequences. In addition, highly toxic bacteria like Clostridium perfringens, Clostridium tetani, and Clostridium botulinum, are the causative agents of gas gangrene, tetanus, and botulism, respectively [220]. Other bacterial groups identified in these soils include Pseudomonas, Mucor, and Aspergillus spp. [215]. Also, microbial groups such as Yersinia enterocolitica, Escherichia coli, Streptococcus faecalis, Helicobacter pylori, and Mycobacteria, have been implicated in the etiology of conditions like Crohn's disease and leaky gut syndrome, which are characterized by severe, chronic inflammation of the intestinal wall [216, 217].

This practice is widespread around the world and has been reported to have economic significance in some places due to the income it generates [216, 221]. Today, there is even a market for geophagy materials as treatments [222]. However, little is known about how clays are produced, managed, and selected. Ethnomicrobiology could address these concerns by conducting continuous monitoring and developing practices to manage these clays, especially given their frequent consumption.

# Microbial-human interaction in traditional medicine and health systems

Modern life has overcome significant health challenges, but it has also introduced new ones. While modern medicine has provided us with antibiotics and hygiene practices that have saved countless lives, it has also disrupted the delicate balance between our bodies as hosts and their microbial inhabitants [223–225]. In recent years, the critical role of the gut-brain axis in maintaining homeostasis has been increasingly recognized, with the microbiota identified as key regulators of gut-brain function [226–228]. This axis is gaining traction in research areas investigating the biological and physiological underpinnings of psychiatric and neurodevelopmental disorders, age-related declines in microbial diversity, neurodegenerative diseases, and social behaviors, as well as facilitating communication

across various animal species, including humans [229–231]. The microbiota and brain communicate through multiple pathways, including the immune system, tryptophan metabolism, the vagus nerve, and the enteric nervous system, with microbial metabolites such as short-chain fatty acids, branched-chain amino acids, and peptidoglycans playing an important role [227]. Numerous factors can influence the composition of the microbiota early in life, including infection, mode of birth delivery, stress, antibiotic use, type of diet, environmental stressors, and host genetics, with microbial diversity decreasing with age [228–230].

Over 100 years ago, Metchnikoff introduced the concept that lactic acid bacteria (LAB) could be beneficial to human health [231, 232]. In his book, The Prolongation of Life, he emphasized the importance of consuming large amounts of these beneficial bacteria. He suggested that modifying the gut microflora with probiotics (beneficial bacteria that can replace harmful microbes) could confer numerous health benefits to the host. Probiotics are described by the Joint Food and Agriculture Organization (FAO) and the World Health Organization (WHO) as live microorganisms that should provide a measurable physiological benefit [233]. Probiotics are typically consumed as part of fermented foods, sometimes with specially added active live cultures, such as in yogurt and soy, or as dietary supplements. However, traditional fermented foods and beverages are also recognized as an important source of these beneficial groups [232, 234-237].

The use of traditional medicines and religious ceremonies in health-related matters among different cultural groups is primarily carried out by traditional healers in indigenous communities and does not necessarily compete with Western medical services [238-240]. Fermented products are also medicinally in various regions to treat gastrointestinal problems. For example, kefir was proposed as a treatment for melancholia in the early 1990s [241]. Nevertheless, traditional healers such as curanderas or curanderos play a crucial role in promoting health therapies in several rural communities in Latin America. Many remedies are plant-based, and many plants produce metabolites that exhibit antimicrobial activity against bacteria and yeasts [242-244]. For example, species such as Piper regnellii have shown good activity against Staphylococcus aureus and Bacillus subtilis, moderate activity against Pseudomonas aeruginosa, and weak activity against Escherichia coli [245-247]. Punica granatum showed good activity against S. aureus [248]. Eugenia uniflora showed moderate activity against both S. aureus and E. coli [249]. Psidium guajava, Tanacetum vulgare,

Arctium lappa, Mikania glomerata, Sambucus canadensis, Plantago major, and Erythrina speciosa have shown varying degrees of antibacterial activity [250–252]. These plants are commonly used in herbal medicine across different regions of the world to address gastrointestinal health issues [253, 254]. In this context, there is a deep-rooted knowledge surrounding the use of plant species that produce metabolites affecting the microbial communities that are part of the human microbiota, positioning traditional healers as effective microbial managers.

In the ontologies of Amerindian, Circumpolar, and Southeast Asian peoples, hallucinations or visions are not dismissed as mere delusions or symbolic constructs. Instead, they are recognized as means of perceptual access to physical reality [255, 256]. For example, shamans of lowland South America claim the ability to diagnose and treat infectious diseases and assess the status of wildlife resources through interactions with pathogens perceived during visions. This phenomenon has often been attributed to neural origins, presumably revealing the underlying workings of the mind. However, Giraldo Herrera [255-257] adds a postulate that may help to understand this phenomenon. He suggests that entoptic microscopy, the perception of one's retinal structures, blood cells, microscopic particles, and occasionally microbes flowing through retinal capillaries may play a key role. In this sense, the shamanic visions may serve as a subjective means of engaging with microbes through these entoptic visions.

To our knowledge, few studies have investigated indigenous peoples' perceptions of microbes. This represents a potential area of study from ethnomicrobiological perspective, aiming understand how people classify microbial to communities within the framework of folk biology, for what we might call an invisible world. It is also crucial to emphasize that ethnomicrobiology does not seek to validate all these practices, but rather to recognize the relevance of the knowledge and practices carried out by curanderos or shamans, rooted in the beliefs of different cultures in different times and places. Ethnomicrobiology can contribute to understanding how human and microbial ecologies shape each other, and how humans and microbes interact and are connected through food, identity, health, and ecological, evolutionary, and political relationships. From this perspective, it is possible to reimagine humans not as isolated entities like Homo sapiens, but rather as dynamic ecosystems, as holobionts [26, 258].

# The dawn of evolutionary Ethnomicrobiology: finding evolutionary patterns in human-microbial interactions

Ethnobiological research has greatly enhanced our understanding of the evolutionary processes that have unfolded over hundreds or thousands of years between humans and plants, animals, fungi, microorganisms, and the ecosystems they inhabit and manage. These humannature interactions have had and continue to have profound evolutionary consequences for the organisms involved, for humans themselves, for their cultures and societies, and for the ecosystems and landscapes of the territories they occupy [259].

explore these To evolutionary perspectives, ethnobiology integrates insights from biological and ecological sciences, as well as social, economic, and anthropological disciplines. Ethnomicrobiology, subfield of ethnobiology, is no exception [260]. The evolution of organisms that interact with humans is often guided by human intentions, creativity, and goals; a process commonly referred to as domestication [261]. However, Darwin recognized in the earliest studies of domestication that unconscious selection often plays an important role in domestication [262]. In the 1980s David Rindos constructed an inspiring theory establishing domestication as a coevolutionary process, and, importantly, introduced the notion of incidental domestication, whereby organisms involved in interactions evolve without a guided, intentional process [263]. More recently, Michael Purugganan has gone further, including in domestication mutualistic interactions between species, not necessarily involving humans. All these theoretical aspects are part of an important debate and guide important research agendas, which are of particular interest for constructing theoretical frameworks to analyze how these processes occur in the interactions between humans and invisible organisms [264]. The fundamental mechanisms that drive the evolution of organisms include the processes that generate genetic variation (such as mutations, genome changes, and recombination at the molecular and chromosomal levels) and the evolutionary forces that shape this variation in populations, including natural and artificial selection, genetic drift, gene flow, and breeding systems [265, 266].

In domestication studies, it is crucial to document the existence of variation, as well as how people apply or determine human selection to this recognized variation. It is also important to examine how this variation is used, valued, and managed differently [259–261]. Adaptation under domestication is a key factor in the success of organisms to thrive and reproduce in human ecological, technological, and cultural contexts [267]. Domestication involves the continuous transformation of organisms

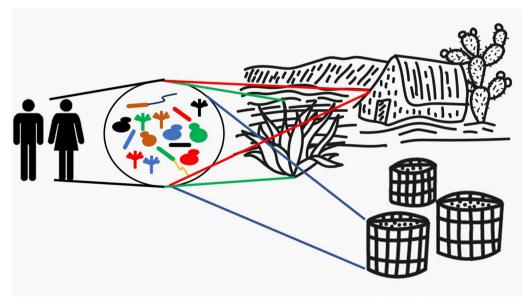
in response to changes in culture, social organization, technology, landscapes, and ecosystems, all of which are highly dynamic processes [268]. Domesticated organisms are generally well-adapted to these contexts and human selection, while natural selection also plays a role in shaping these adaptations [266].

Ethnobiological studies with an evolutionary approach have been essential in understanding the principles of change involved in the interactions between humans and the biotic components of ecosystems and landscapes [267]. This approach provides a framework for studying the evolution of organisms and landscapes as shaped by human influence (Fig. 3). But what can ethnomicrobiology have to offer to biological and cultural evolution? What are the future perspectives for microbial selection, contexts of fermentation, and soil management? Do these human actions have evolutionary consequences for microorganisms? These are all questions that need to be explored and that ethnomicrobiology can help to answer.

To advance studies in evolutionary ethnobiology and cultural evolution within microbial communities, we strongly recommend that future research adopt a multispecies relational approach. This approach addresses the intricate relationships between species and how they co-create and influence each other [268].

These dynamics are vividly illustrated in agricultural and fermentation systems. For example, in the production of fermented beverages, the plant substrate provides sugars that fuel microbial fermentation. Before this, plants have already interacted with other species in their environment. Once fermentation occurs, the humans who manage the process interact with a final product that is the result of the collaboration and co-creation of a diverse community of beings [268, 269].

In this context, food cultures and biodiversity are not merely processes where microbes, animals, and plants come together and flourish; rather, biodiversity becomes a web of relationships and interactions, each with its narrative [269, 270]. Another important consideration in these studies is that mere observation and tactile interaction are insufficient to fully grasp the ever-changing nature of fermentation and agricultural processes, where microbial communities are never in a fixed state. It is essential to continuously sense and respond to the evolving multispecies possibilities within these transformations. Our senses should operate within a reciprocal multispecies context [271]. As much as sensing is crucial in these practices, our engagement with multispecies assemblages also shapes and enhances our sensory perceptions. Our cultural background also plays



**Fig. 3** Ethnomicrobiology, when viewed through a Darwinian evolutionary lens. Ethnomicrobiology can provide valuable insights into the processes of microbial management, selection, and domestication, particularly within microbial communities involved in intentional fermentations. Humans, represented by the black lines, act as key facilitators of microbial management and creators of new ecological niches. For example, the establishment of specialized facilities designed to collect microbial communities and promote fermentation (red lines). Similarly, fermentation vessels, represented by blue lines, provide environments where fermentation-related microbes are harbored, cultivated, or recruited to produce fermented beverages. Ethnomicrobiological studies also shed light on how the domestication of plants and animals reshapes their associated microbial communities, such as the microbiomes of domesticated plants (green lines). These ongoing human-microbial interactions contribute to niche construction over time and can even transform larger landscapes

a key role in determining what is considered acceptable or unacceptable.

### Microbial domestication in fermented products

While scientists have made significant progress in understanding the domestication of crops and livestock, the domestication of microorganisms remains less well understood. Nevertheless, it is an emerging field of study that is likely to force society to rethink assumptions about the evolution of human food systems. Following the so-called agricultural revolution, the domestication of bacteria, yeasts, and molds became critical to human food systems, enhancing the stability, quality, flavor, and texture of various products [272]. However, the practice of processing foods from wild relatives of cultivated plants likely predates agriculture. Today, various strains of yeast and bacteria associated with fermented products exhibit traits suggesting domestication. For instance, genomic and phenotypic studies suggest that wild species of Lactococcus likely originated in plant environments. Changes in these species occurred as they were propagated over generations in dairy environments, with human influence contributing to these new niche conditions [273]. Similarly, extensive research has been conducted on yeast strains of Saccharomyces cerevisiae, a model organism closely associated with human activities, particularly in the production of alcoholic beverages [274] (In Fig. 3 the blue lines represent the creation of these new conditions).

Several strains of S. cerevisiae exhibit genetic and phenotypic differences from their closest known relative, S. paradoxus, leading to the hypothesis that S. cerevisiae is a domesticated species specialized for fermenting alcoholic beverages. Isolates of S. cerevisiae from other environments are thought to represent migrants from fermentation sites, although their exact migration routes remain unclear [275-277]. While genetic and environmental variation in S. cerevisiae strains related to bread, wine, and beer production has been characterized, little is known about the mechanisms and processes of human-driven selection [278, 279]. Ethnomicrobiological research could help fill these gaps, as the management of microbial communities remains an underexplored area. Traditional knowledge about microbial management is often underestimated, but practitioners around the world engage in various practices that maintain microbial communities, especially in the production of culturally significant products [280, 281]. These practices include small but critical details, such as preserving autochthonous microbial communities in containers [282, 283], continuously feeding starter cultures with high-quality sugars [284], and storing batches for future fermentations [281, 285].

While microbes lack the visual phenotypes that drive selection such as in plants and animals, selection can still occur through other traits. Specifically, sensory traits such as smell, taste, and texture. These sensory traits, often overlooked in traditional domestication studies, are particularly relevant to microbial communities. Traditional fermenter's preferences for specific sensory traits may act as a selection mechanism guiding the domestication of microbial communities at both population and community levels. Although research on the domestication of bacteria [286, 287], yeasts [288], and molds [289, 290] has advanced, human management of food production has created new ecological niches. The abundance of agricultural and non-agricultural food sources allows microbes to thrive in environments where their metabolic requirements are predictable. This consistency has led to rapid genomic specialization through processes such as pseudogenization, genome decay, interspecific hybridization, gene duplication, and horizontal gene transfer [289]. However, the specific practices and processes by which traditional managers influence microbial selection remain largely unclear.

Ethnomicrobiological studies can shed light on the history and evolution of microbial diversity and provide new perspectives on how selection occurs. A key question that these studies can address is whether microbial domestication is a conscious or unconscious process. Detailed analysis of practices and preferences through ethnographic studies could help us better understand the complexity of microbial selection. Furthermore, population genomics and phylogenomic approaches could be used to trace the origin and frequency of domestication events. In addition, metagenomic sequencing of ecological niches could identify microbial groups selected by human practices and reveal how changes in the fermentative environment can influence microbial evolution. These activities may promote preadaptations such as temperature tolerance, flavor molecule production, carbon metabolism, and spoilage control [288, 289].

Further comparative studies of the chemical fingerprints of fermented products, such as aroma, flavor, and texture, using techniques like High-Performance Liquid Chromatography (HPLC), combined with microbial community analyses, could enhance our understanding of the impact of sensory attributes on microbial domestication. In addition, assessing producer preferences during the fermentation process or in the final product could provide insights into how microbial selection occurs through sensory attributes. Finally, microbial studies that incorporate an ethnobiological perspective can provide valuable insights into the

mechanisms underlying microbial selection and domestication.

# Niche construction: the intertwined process of dwelling places for microbial assemblages

The Niche Construction Theory (NCT), part of Evolutionary Extended Synthesis, presents additional evolutionary mechanisms beyond genetic inheritance. NCT is particularly appealing for studies of domestication and species closely associated with human cultures because it considers how ecological and cultural processes influence evolutionary dynamics and contribute to the stability of environmental conditions across generations [291–293]. These cultural processes are manifested through interactions with other species and ecosystems, as well as through strategies for environmental modification. Human actions and cultural developments also shape the future of populations and promote evolutionary change [294-296].

According to Odling-Smee [297], the evolutionary niche encompasses the selective pressures exerted on a population. The presence of human cultures has consistently modified numerous niches, with social and ecological consequences for both humans and other organisms. These evolutionary processes are not limited to changes in genetic fitness but are expressed through cultural technologies, behaviors, memory, history, reflecting intergenerational environment relationships. The application of NCT to microorganisms is particularly relevant in the context of ethnomicrobiology. Microbes collectively shape their environment in profound ways through their metabolic products, influencing and altering their shared habitat, a process that can be understood through the lens of niche construction. For example, microbial niche construction may involve the production of biofilms, and the release of enzymes, toxins, or metabolites that alter the composition of the microbiome. Some of these traits can be considered extended phenotypes, where microbes actively modify their environment for their benefit and potentially for the benefit of others [298].

One of the most tangible examples of microbial niche construction in everyday life is within our food systems, particularly in the creation of fermented foods. Products such as cheese and alcohol are transformative processes, orchestrated by microbes that are often invisible to the naked eye, yet present everywhere: in the air, on insects, plants, houses, tools, and in every inch of soil [84, 299]. In addition, humans have fostered and designed new environments for these microbes, building structures and landscapes that facilitate microbial growth. These organisms, in turn, create microenvironments that can

later be perceived through the sights, tastes, and smells of our foodscapes [70, 300–303].

Since the advent of cereal agriculture, new niches have become available for microbial communities, allowing them to utilize these novel substrates. Humans have also developed tools, containers, and specialized facilities essential to the production of fermented products, all of which serve as critical sites for microbial assembly and activity [70, 302, 303]. Practices such as cleaning equipment and containers play a key role in maintaining specific microbial communities within fermentative environments [22, 70, 281, 302, 303] (in Fig. 3, this idea is represented by the red lines, where specific facilities for microbial *dommus* are established).

Numerous studies have demonstrated the contribution of NCT to human nutrition, particularly in understanding how food storage and processing evolved during the Neolithic period. These developments, along with advances in skills, knowledge, and technology, have increased human survival rates [304]. Heritable cultural practices (such as fermentation) have conferred significant evolutionary advantages, reinforcing the role of cultural inheritance in human evolution [305].

In this way, organisms actively shape their environment through their life activities [306]. This environmental modification, known as ecosystem engineering, exerts selective pressure not only on the species itself but also on neighboring species, a process referred to as niche construction [307]. Within the ethnomicrobiological framework, future research could explore how the construction of microenvironments alters the broader macroenvironment, and vice versa. For example, microorganisms in fermented products are excellent niche builders, but they also exist in symbiosis with humans, who create favorable living conditions for them by providing containers and facilities that support their growth.

### Microbial evolution associated with domesticated crops

Macroorganisms are colonized by microbial communities that perform crucial biological and ecological functions for their hosts. The composition of these microbial communities is often under host control [308]. In domesticated organisms, such as crop plants, both human and natural selection exerted by the agricultural ecosystem play a role [309, 310]. While plant domestication has long been recognized to promote changes in genetic diversity, plant physiology, and morphology, the subsequent effects on associated microbiome communities have been less extensively studied. Domestication can influence these microbial communities, resulting in what has been described as "an ecosystem on a leash" [311-313]. For example, domesticated plant genotypes have been shown to modulate soil microbiota by selecting specific microbial communities in the rhizosphere compared to their wild and semi-domesticated counterparts [314, 316] (this idea is represented in green in Figure 3).

Studies on different *Phaseolus* species illustrate these differences and document shifts in microbial communities from wild to domesticated genotypes [317, 318]. These studies have generally observed changes in the abundance of specific microbial groups, such as increased *Actinobacteria* in domesticated plants, and higher levels of *Proteobacteria*, *Acidobacteria*, and *Firmicutes* in wild genotypes. Furthermore, the complexity of microbial community networks in the rhizosphere tends to decrease from wild to domesticated genotypes, indicating a reduction in the robustness and connectivity of these networks [318].

This knowledge of plant domestication is often intertwined with soil management practices. For instance, Barrera-Bassols and Zinck [31, 185], in their global survey of ethnopedology, reported that local soil knowledge often arises in regions with high levels of plant and animal domestication, such as China, India, Mexico, and Egypt. Therefore, soil management and plant domestication may form a complementary link between the kosmos (beliefs, cosmovisions), corpus (environmental knowledge), and praxis (practices) of local land users and farmers [319, 320]. Ethnomicrobiology, with its inherent transdisciplinary approach, could serve as an integrative scientific field to help us understand how these biocultural approaches and practices in soil management and plant domestication are interrelated. This understanding could inform the development of sustainable practices for soil management and agriculture in the face of challenging environmental conditions.

Ethnomicrobiology could also provide theoretical perspectives on microbial domestication within the context of domesticated plants and other organisms. For example, plants may adapt to their environment by hosting beneficial bacteria that provide selective advantages under stressful conditions. Endophytes, a class of beneficial bacteria that live inside plants, can enhance plant nitrogen use efficiency, a critical factor for plant growth, especially in cereal crops [321]. A striking example is the geographically isolated maize landrace known as "Olotón," grown in the Sierra Mixe region of Oaxaca, Mexico. This maize utilizes atmospheric nitrogen by developing an extensive network of mucilagesecreting aerial roots that harbor diazotrophic (N2-fixing) microbiota capable of incorporating atmospheric nitrogen [322]. A study by Dumingan [323] investigated whether this microbiome trait is shared among closely related maize varieties in the region. The results showed the presence of multiple root endophyte species in each maize relative, with these strains being vertically transmitted to new generations, possibly through seed. However, the selective breeding of maize under high-nitrogen conditions to create modern varieties may have caused the plant to lose these beneficial bacteria that allowed wild maize ancestors to thrive in low-nitrogen soils. These microbial communities hold significant potential for reducing the reliance on nitrogen fertilizers. However, this potential raises critical questions regarding the commercialization of biotechnological applications by large industries versus the ethical recognition of these microbes as a shared common good within local agrobiodiversity.

### Ethnomicrobiology and critical social perspectives

Ethnobiology actively challenges colonialism, racism, and social injustice by promoting the decolonization of institutional structures, research projects, and even ethnobiologists themselves [5]. Ethnomicrobiology aims to establish itself as a field focused on the interactions between humans and microorganisms. Within this approach, it is crucial to recognize that microorganisms have both a future and a past that are inextricably linked to human involvement in ecological, political, and economic networks [324]. Over the past halfcentury, humans have profoundly transformed the world, particularly through economic growth models, industrialization, population growth, increased resource consumption, energy use, and the resulting pollution, a phenomenon collectively referred to as the Great Acceleration [325-327]. In the face of these changes, a critical question arises: What are the impacts of the Anthropocene on the microbial communities associated with human existence? Scientists have begun to address this question, highlighting the problematic nature of human microbiomes and the growing concern about microbial resistance [328]. In the context of Anthropocene studies, non-human entities, including microbes, are increasingly recognized as social actors with significant implications for economics, bioethics, and natural resource management. This recognition leads to new dialogues and questions: How should we conceptualize the relationships between microorganisms and humans in the Anthropocene? What are the conditions and challenges for these relationships?

A key challenge for ethnomicrobiological studies in the Anthropocene is to rethink the dynamic relationships that microorganisms establish with humans. This requires reconfiguring the dominant narrative that often relegates microorganisms to the role of mere disease vectors, ignoring their significance within evolutionary and co-evolutionary frameworks [329]. Recognizing

microorganisms as active agents in critical societal developments allows us to see them as entities that evolve alongside humans, historically shaping and being shaped by human existence [330]. In the following sections, we propose several key issues that ethnomicrobiology from a social perspective should address.

### **Biopiracy in microbial communities**

Microorganisms play a critical role in biological diversity and are recognized, managed, and used for various purposes in different cultures. Since 1992, the *Convention on Biological Diversity* (CBD) has promoted the sustainable use of resources and the fair and equitable sharing of the benefits arising from the use of genetic resources [331]. To date, 196 countries have ratified the Convention, which covers the full spectrum of biological diversity, including ecosystems, species, and genetic variation. However, significant uncertainties remain regarding its implementation at the microbial level, mainly due to the vast, largely unexplored diversity of microbial species, their distribution, environmental stability, and complex interactions with other species, including humans [332].

The Nagoya Protocol aims to ensure the legal use of genetic resources, facilitate benefit-sharing, and impose penalties for violations [333]. Despite these goals, microbial resources have been largely overlooked, even though the relationship between microbial communities and human cultures is as old as the domestication of plants and animals [35, 272]. A major challenge is the characterization and definition of microbial species, especially among diverse bacterial groups. Microbiologists view bacteria as existing on a continuum of varieties, with species classification traditionally based on DNA reassociation, where strains with at least 70% reassociation are considered to belong to the same species [334]. In addition, newer culture-independent techniques, such as next-generation sequencing, propose a paradigm shift, suggesting species assignment based on 95% genomic identity for bacterial groups [276]. This complexity in bacterial species identification was not fully addressed in the Nagoya Protocol, making it a challenging issue.

The Protocol must evolve in order to properly value genetic resources and traditional knowledge, especially from the most biodiverse regions. The Protocol must ensure equitable benefit-sharing with communities that have long managed and generated this knowledge, even when it is not immediately apparent [332]. This is especially relevant for microbial communities associated with human activities, such as the production of fermented products, which involves deliberate management actions rooted in traditional

ecological knowledge, including the selection of specific microbial communities or even particular strains [272, 289].

As noted above, humans actively select and cultivate microbial communities to achieve desired product characteristics. As a result, bacterial and yeast communities can develop unique traits due to selective human management. These human-associated microbial groups are part of evolutionary and domestication processes that are shared and promoted by humans, such as traditional fermentation managers and farmers who maintain these microbial and macroecosystems [281]. While bacterial communities may exhibit similarities due to the broad definition of species, yeast communities are characterized by distinctive traits and genomic regions selected and associated with these human-managed environments [276, 288, 335, 336].

The incentives provided by the Nagoya Protocol and the Convention on Biological Diversity for the protection and sustainable use of biodiversity by recognizing the value of genetic resources and associated ecological knowledge should be applied with careful attention to biopiracy concerns, particularly with respect to managed microbial communities such as in the case of Oloton maize [337, 338]. Microbial cultures are more easily moved, appropriated, and commodified for private profit than plants or vertebrates, making the risk of microbial piracy very real. According to Bravo [339], the potential profitability of a product increases by 400% when the biological (genetic) resource is linked to local knowledge, leading to bioprospecting projects and biopiracy affecting living organisms and local communities throughout Latin America [340]. Gaps in the establishment and the application of national and international laws regarding microorganisms make them easy targets for patenting, along with their genetic material and biophysical activity, to become the subject of patents by private companies, with significant conservation impacts.

Over the past decade, corporations have increasingly gained control over the Earth's biodiversity and Indigenous knowledge through new property rights, often leading to monopolization rather than fostering genuine innovation [340]. Patents on living resources and indigenous knowledge have effectively privatized the biological and intellectual commons. Life forms are often redefined as "products" or "machines", reduced to their genetic components or the outputs derived from such "machines". However, microorganisms must be recognized in regulations as living organisms, whose metabolism, presence, and development are vital to humans and play an integral role in human perception, use, and interactions [341]. It is also critical to consider the immense value of microbial communities and the

importance of responsible management of microbial resources.

Culture collections are invaluable resources for the sustainable use and conservation of microbial diversity. Several countries have also invested in gene banking their microbial cultures, particularly those used in the fermentation of traditional foods and beverages. Advances in biotechnology have further enhanced the importance of these collections, some of which have been recognized by the International Depositary Authority (IDA) for the deposit of patent cultures. Notably, the Budapest Treaty, adopted in 1977, addresses a key issue in the international patent process: inventions involving microorganisms. All contracting states are required to recognize microorganisms deposited with an IDA as part of the patent disclosure procedure [343, 344]. However, as mentioned above, parts of this legislation remain ambiguous. Consequently, much work remains to be done to address the microbiological agenda, where ethnomicrobiological research can provide valuable insights and advocate for the development of local and international policies to address pressing biopolitical concerns.

Given the significant economic impact of such patents, ethnomicrobiologists must address these concerns in future research agendas. Responsible management of microbial communities is essential, not only to prevent monopolization, but also to ensure equitable distribution of the benefits derived from these valuable resources. Biopiracy and the patenting of microorganisms and their metabolic products pose a serious threat to local populations who have the knowledge and skills to cultivate, harvest, manage, and maintain microbial communities. These practices not only threaten the livelihoods of these communities but also threaten the biodiversity of species that have co-evolved with traditional fermenters and farmers. To date, local and traditional knowledge can be exploited and patented, fueling a new wave of biopiracy.

While some progress has been made in recognizing microorganisms as part of nature, a critical gap remains in recognizing them as part of biocultural landscapes and the intangible heritage of indigenous farmers, brewers, tanners, cheesemakers, and fermenters. Currently, there is a notable lack of policies that affirm the rights of traditional custodians of microbial cultures or the rights of the microorganisms themselves. This largely unaddressed ethical and legal issue requires urgent attention from policymakers, especially considering the rapid expansion of commercially motivated bioprospecting projects.

# Landscapes of fermentation and social justice: from micro to macro social change

According to the World Economic Forum (WEF), humanity's current production systems will not be able to meet the future demand for protein or achieve the eradication of hunger, key objectives of the Sustainable Development Goals. This is a complex and controversial issue that is beyond the scope of this reflection. However, fermentation has emerged as a promising frontier for alternative protein production [342, 345]. In recent years, several innovative initiatives have explored new protein sources [345-347]. Techniques such as precision fermentation, which uses engineered microbes to produce large quantities of proteins typically found in animal products without the need to breed, feed, or slaughter animals, are gaining traction [347]. The core idea is to remove animals from the production system, thereby reducing the risk of contamination, eliminating the need for antibiotics, and reducing the threat of crossspecies disease transmission [347].

While advances in fermentation technologies depend on adequate funding and expertise, it is critical to recognize that these technologies remain out of reach for many communities. The World Economic Forum (WEF) emphasizes that fermentation holds the potential to fundamentally transform the way the world eats, but significant investment is still required to realize this potential. While companies have developed promising fermentation technologies, these innovations are still in their early stages, underfunded, and primarily concentrated in countries with established economies. In addition, most fermentation facilities are designed for industries other than alternative protein production [348]. In contrast, traditional fermentation has long been a practical, localized activity that provides essential nutrients, including proteins, probiotics, prebiotics, and other vital components, making it a cornerstone of local diets worldwide. These traditional practices often play a key role in helping communities protect their environments.

Ethnomicrobiology can also address important social justice issues related to fermented products. Many fermented beverages today are rooted in colonial commodities with complex histories and uncertain futures. This phenomenon is vividly illustrated, for example, by the tequila industry and the production of mezcal and other distillates in Mexico [78]. Tequila, a distilled beverage, is legally required to be made from a single highly homogeneous clone of *Agave tequilana* Weber variety azul. In 2006, UNESCO declared the blue agave fields and distilleries to be part of the *Cultural Heritage of Humanity* in the category of *Cultural Landscapes* [349]. However, *A. tequilana* 

monocultures degrade local agroecosystems [350] and differ significantly from the more sustainable biocultural landscapes where other distilled beverages such as the traditional mezcales produced in Mexico. This loss of genetic diversity in both plants and microbial cultures [351, 352], as well as vulnerability to pests and diseases, intensive agrochemical use, soil erosion, water contamination, and damage to the health of the local population, are direct consequences of meeting the international demand for tequila [353–355]. Many have called for UNESCO to reconsider its designation because the tequila landscape does not meet the standards of other recognized cultural landscapes.

Historically, landscapes have been transformed to produce alcohol as a commodity [367], often resulting in significant homogenization, with only a few species remaining. For example, more than 1500 grape varieties have been recorded, many of which are Indigenous, ancient landraces adapted to their environment, but modern vineyards are now dominated by the ubiquitous *Cabernet Sauvignon* grape [299, 300]. This homogenization extends beyond the landscape to the microbial level, where also microbes become less diverse. In contrast, the microbial richness of traditional cheeses, wild wines, or spirits like mezcal manifests in a sensory explosion of flavors, textures, and aromas that reflect the complex microbial metabolism at work [78].

Processes such as fermentation offer valuable insights into how micro-scale activities affect macro-scale environments, such as landscapes. These landscapes are not simply geographic or geological spaces but are complex constructions shaped by interactions between biological (including microbial), sociological, geographic, and economic factors. Ethnomicrobiology, as a science committed to both social and environmental justice, can propose strategies to support fermenting producers resist the homogenization of food, and promote food sovereignty. It calls for actions that incorporate diverse perspectives, values, and behaviors, to ensure a more just and sustainable future for fermented food systems.

### **Conclusions**

Ethnomicrobiology provides a unique scientific space that acknowledges the symbiotic relationships between microorganisms and humans and emphasizes the cultural specificity of these interactions. The emerging approach provides a platform for exploring the diversity of life forms as analyzed from the biological sciences and microbiology. While modern science first explored the microbial world in the seventeenth century, many human communities had long recognized the presence of these microorganisms through external indicators, identifying

them by their properties, attributes, and outcomes under different cultural contexts.

Ethnomicrobiology compels us to see microorganisms cultural, biopolitical, economic, ecological, evolutionary, and social agents, deeply intertwined with human existence. By recognizing humans as part of multi-species communities (holobionts composed of interacting genomes) this approach promotes a broader evolutionary perspective on microbial evolution, including that associated with management that can be considered domestication. It also challenges long-held assumptions about the diversity of ways humans coexist with microbes in different cultural contexts. It highlights the importance of treating these microorganisms as natural resources, protected by the same international and national laws that protect plants and animals. Microbes are an integral part of agrobiodiversity, and their value goes beyond mere commodification. However, indigenous and local knowledge of microbial management is often undervalued.

Because microbial management plays a critical role in supporting healthy diets and sustainable agroecosystems, ethnomicrobiologists need to establish clear short-, medium-, and long-term goals for maintaining and enhancing the systems in which microbial management occurs. In doing so, they can develop diagnostic and comparative studies to inform future applications and deepen our theoretical understanding of microbial-human interactions.

the successes in applying traditional knowledge, the dominance of a single scientific paradigm (compounded by political and socioeconomic barriers) has often led to the marginalization of local microbiological expertise and its custodians. These issues have not only devalued local knowledge but also exacerbated the exclusion of these communities. It is for a conceptual, theoretical, and integrative phase in ethnomicrobiology that invites collaboration and the establishment of bridges between ethnobiologists, microbiologists, and other disciplines. interdisciplinary and transdisciplinary approach will promote a deeper understanding of human-microbe interactions and protect them from biopiracy and other threats.

Ethnomicrobiology broadly calls for transdisciplinary collaborations and respect for the original caretakers and artisans who manage microbial cultures. It advocates the decolonization of scientific inquiry by affirming the intrinsic rights of microorganisms and honoring the sovereignty of the peoples who have historically managed them. It also advocates a shift from ethnocentric to biocentric perspectives,

embracing what Darwin called "the entangled bank" the complex web of relationships that contribute to the richness of human and non-human life, as well as the diversity of foods, beverages, fibers, medicines, and agroecosystems that shape our material culture.

### **Abbreviations**

LAB Lactic acid bacteria NCT Niche construction theory

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### **Author contributions**

All authors contributed to this study. The main concept for the article was developed by César Iván Ojeda Linares, Gary Paul Nabhan, and Alejandro Casas. Material preparation and data collection were carried out by César Iván Ojeda Linares, Tania González, and Alejandro Casas. César Iván Ojeda Linares and Tania González wrote the initial draft of the manuscript, with all authors providing feedback, reviewing, and editing subsequent versions. All authors have read and approved the final manuscript.

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### Data availability

No datasets were generated or analysed during the current study.

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### Ethics approval and consent to participate

Not applicable.

### Consent for publication

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### **Competing interest**

The authors declare no competing interests.

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