Edible mycorrhizal fungi of the world: What is their role in forest sustainability, food security, biocultural conservation and climate change?

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Funding information
Mexican Council of Science and Technology (CONACYT); National Natural Science Foundation of China, Grant/Award Number: 31961143010; Open-Funds of Scientific Research Programs of State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Grant/Award Number: A314021402-2002

Societal Impact Statement
Edible mycorrhizal fungi (EMF) have been consumed since ancestral times by humans either as food, medicine or for ceremonial use. Nowadays, they are a non-timber forest product and a diverse genetic resource with great ecological, sociocultural, economic, medicinal and biotechnological relevance around the world. Therefore, they have a paramount role to play in meeting the United Nations global sustainable development goals 2030. EMF may promote forest sustainability, biodiversity conservation, mitigation of greenhouse gas emissions through the maintenance of forest masses, human nutrition and health, economic development, conservation of biocultural heritages, women empowerment and hunger mitigation. We provide a worldwide review of the knowledge, biodiversity, novel approaches, future challenges and perspectives in the post-COVID era of this important genetic resource whose relevance has usually received marginal attention despite its strategic global significance.

Summary
Ectomycorrhizal fungi play a key role in the structure and functioning of forest ecosystems. They have a paramount importance in nutrient cycling, plant protection against pathogens and abiotic stress, and establishment of underground networks that connect trees and other plants in nature, therefore being the 'internet' of the forests. According to our literature review, globally 970 mycorrhizal fungal species (including both mushrooms and truffles) are edible, and they have enormous relevance either as a source of subsistence in low-income human groups around the world or as an important economic component whose international commerce is worth billions of American dollars annually. Since edible mycorrhizal fungi (EMF) are a non-timber forest product, their sustainable use and management is crucial in order to maintain forest stands and to provide well-being to the human communities surrounding the forested areas where they grow. In different parts of the world, different cultures have developed a traditional knowledge of EMF over
INTRODUCTION

Due to their unique morphological, ecophysiological and phylogenetic characteristics, fungi form the second largest group of organisms on Earth, only outnumbered by insects. They have a cosmopolitan distribution and have colonized all terrestrial and aquatic ecosystems. Their diversity has been estimated to range between 2.2 and 3.8 million species (Hawksworth & Lücking, 2017). Despite the fact that in nature they establish a trophic continuum, according to biotic and abiotic conditions, three trophic groups are recognized: (a) saprotrophic, when they use organic debris as their main source of energy; (b) parasitic, when they invade other living beings causing damage to them, in order to survive; and (c) mutualistic, when they establish beneficial symbioses, sharing benefits with other organisms to survive. In forest ecosystems, one of the most important structural and functional biotic components is the mutualistic fungi forming mycorrhizal associations with plants. A smaller group of fungi belonging to the Glomeromycota forms arbuscular mycorrhiza with the majority of land plants, but they do not produce fruiting bodies. It is the larger group of fungi belonging to Basidio- and Ascomycota that establish ectomycorrhizal symbioses and produce edible mushrooms and truffles. They are crucial in ecosystem health maintenance and nutrient cycling. Through this ectomycorrhizal association, plants augment their fitness by enhancing their nutrition and increasing their survival under stressful conditions, including pathogen attack, potential toxic elements, drought and high temperatures (Smith & Read, 2008). These benefits are mainly due to the mantle in the case of pathogen protection; and mainly to the external mycorrhizal mycelium, which is the link that connects the soil and plant components in forest ecosystems (Read & Pérez-Moreno, 2003). It has been estimated that in three square meters of forest soil there is enough ectomycorrhizal mycelium in length to span the Earth’s equator (Pérez-Moreno, 2005). Ectomycorrhizae connect trees, establishing the so-called wood-wide web, equivalent to an ‘internet’ in the forest, through which nutrients and, potentially, signals; are shared among trees belonging to a range of different taxonomic groups (Sen, 2000). Recently, it has been estimated that 60% of the trees on Earth establish ectomycorrhizal symbiosis (Steidinger et al., 2019). The ectomycorrhizal symbiosis evolved several times by independent convergence of different plant and fungal lineages. Its origin dates back to the mid-Jurassic in the Laurasia continent, associated with Pinaceae (Strullu-Derrien et al., 2018), and the oldest known fossils date to 52 million years and were found in India in a tropical broadleaf forest of the Lower Eocene (Beimfore et al., 2011).

Additional to their evolutionary and ecophysiological relevance, ectomycorrhizal fungi constitute an important world biocultural heritage (see Box 1). They have been used at least since the Stone Age by humans as food (Power et al., 2015), and as medicine or sacred elements (Vajda, 2012) in numerous cultures around the world (Pérez-Moreno, Guerin-Laguette, Flores-Arzú, & Yu, 2020). The medicinal properties of EMF (see in Box 1) have been recently tested and confirmed through numerous chemical studies, which currently constitute a relevant frontier research field. Therefore, EMF can be regarded as living repositories of pharmacologically active chemicals. In more than 100 EMF species, analgesic, anti-inflammatory, antinociceptive, antioxidant, antipyretic, antiviral (including anti-HIV), cholesterol-lowering, hepatoprotective and immune enhancement properties have been found (reviewed in Pérez-Moreno & Martínez-Reyes, 2014). The ceremonial use of one of the most iconic ectomycorrhizal mushrooms, Amanita muscaria, by different ethnic groups in Siberia was first documented in 1658 by a Polish war prisoner (Vajda, 2012; von Strahlenberg, 1738). Later, the use was also reported from other regions in the world (e.g., Wasson & Wasson, 1957). However, the most relevant world-wide use of ectomycorrhizal fungi is as food source. EMF are ranked to be richer by percentage dry mass than most food sources in terms of high quality proteins, micronutrients and vitamins. Despite having high nutritional attributes, EMF contain low cholesterol, carbohydrates and triglycerides. In addition, they are an important source of bioactive compounds with medicinal properties. For this reason, they have been considered as important functional foods (see for example Cheung, 2010; Kalac, 2013; Leal et al., 2013). Since ancestral times, EMF have contributed to mitigating the protein malnutrition and micronutrient deficiency for hundreds of thousands of rural families living in nearby forests. These human groups are frequently made up of vulnerable people including young children, lactating and.

KEYWORDS
biocultural heritage, ectomycorrhiza, food diversification, fungal diversity, global Change, truffles, United Nations Sustainable Development Goals, wild edible mushrooms
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BOX 1 Glossary of terms

Bioculture: Combination of biological and cultural factors that affect the behaviour of a human group.

Edible mycorrhizal fungi: This name refers to a group of fungi that form different types of mycorrhiza (mainly ectomycorrhiza but not only), a symbiosis between plant roots and fungi. The fruiting bodies that these fungi produce are an important source of food in different cultures around the world. They include both mushrooms and truffles, i.e., epigeous and hypogeous fruiting bodies, respectively.

Ethnomycology: Discipline that studies the relationships between fungi and human cultures.

Japanese shoro: An economically important edible ectomycorrhizal mushroom with biocultural importance in Japan, whose scientific name is Rhizopogon roseolus (Corda) Th. Fr.

Matsutake: Common name for one of the most highly prized wild edible mushrooms in the world, highly appreciated in Japanese cuisine due to its aroma and texture. Its scientific name is Tricholoma matsutake (S. Ito & S. Imai) Singer.

Milk caps: Common name for a group of mushrooms that exude a latex or milk when cut belonging to the genera Lactarius, Lactifluus and Multifurca. Milkcaps occur worldwide and include some highly appreciated edible ectomycorrhizal mushrooms.

Mycogastronomy: Practice and study of the preparation of dishes that include edible mushrooms, ranging from traditional foods to gourmet cuisine.

Mycotourism: Activity related to harvesting fungi and catering for tourists who wish to experience the contact and knowledge of wild fungi in their natural habitats, while potentially minimizing disturbance of natural areas.

Mycosylviculture: Development and application of forest management techniques to maintain or enhance the production of wild edible mushrooms.

EMF have been consumed as food since ancestral times by different cultures around the world. Evidence has been found that Stone Age humans ate EMF. Power et al. (2015) provided evidence that in the Upper Palaeolithic in northern Spain, humans ate a variety of vegetables and mushrooms. Spores of Agaricales and Boletales (specifically boletes, that are EMF) were identified in a tooth plaque of a 35 to 40-year-old woman. These remains were dated to be 18,700 years old (Straus et al., 2015). In addition to this robust evidence, around two millennia ago, Plinius, in his classic Natural History (Naturalis Historia) written in Latin and published between 77 and 79 AD, mentioned wild edible mushrooms. In his book VI, the chapters 46 and 47 are entirely devoted to mushrooms. In his book XVI, at the end of Chapter 11 he says “… Such is the multiplicity of those products borne by the robur [referring to oaks] in addition to its acorns; and not only these, but mushrooms as well, of better or worse quality, the most recent stimulants that have been discovered for the appetite…”. In the mid-nineteenth century, Bostock and Riley (1855) considered that Plinius referred to well-known edible ectomycorrhizal mushrooms already eaten by the romans mentioning that “… These were the “boletus” and the “sullus” the last of which seem only to have been recently introduced at table in the time of Pliny…”. Currently 970 species of EMF have been reported to be consumed in the world (Figure 1; Table S1). Only nine genera account for more than half of the total reported species number: brittlegills (Russula); milk caps (Lactarius and Lactifluus; see Box 1); coral fungi (Ramaria); Amanita; Suillus; Tricholoma; chanterelles (Cantharellus); and truffles (Tuber) (Figure 1). This trend is similar in the two most important active biocultural mycophilic centres of EMF in the world, where there is also access to trustable bibliographic sources of abundant human EMF consumption nowadays: China (Wang et al., 2020; Wu et al., 2019; Yu et al., 2020) and Mexico (Garibay-Orijel & Ruan-Soto, 2014; Pérez-Moreno et al., 2010; Villareal and Pérez-Moreno, 1989). These two countries harbour a great cultural diversity that includes 51 and 68 ethnic groups, and 1020 and 450 edible wild mushrooms used as food, respectively, whose mycological traditional knowledge generated through millennia is kept alive (and is currently
subject to a growing scientific interest), along with their own cultures, languages, world-visions and natural resources management constituting a living global biocultural heritage. In the case of China, the eight most abundant genera (*Russula*, *Lactarius*, *Lactifluus*, *Boletus*, *Ramaria*, *Suillus*, *Tricholoma*, and *Hygrocybe*) account for 53% of the total EMF consumed in the country (Figure 2a). In Mexico, *Ramaria*, *Amanita*, *Boletus*, *Russula*, *Lactarius*, *Lactifluus* and *Suillus* account for 55% of the total EMF currently eaten in the country (Figure 2b). This evidence shows that the species distribution of EMF consumed in the world is concentrated in only a few genera. Smith and Bonito (2012) reported that there are 82 genera of EMF, 78% of them belonging to Basidiomycota and only 22% to Ascomycota. Among them the *Boletus*, *Russula*-Lactarius-Lactifluus and *Tuber*-Helvella phylogenetic lineages harboured the highest diversity of the known EMF genera. However, we need to highlight that the information related to the diversity of mushrooms consumed in the world, particularly in low-income countries, is far from complete. Some of these areas are underexplored and new species remain to be described. The need for assessment of the diversity and associated ethnomycological information is urgent, especially in areas where deforestation and cultural erosion are happening at a speed never seen before.

According to The State of the World’s Forests 2018 published by the United Nations (FAO, 2018) around 40% of the rural population that are in extreme poverty, live nearby forested areas. In a number of countries, rural populations who live nearby forests are able to distinguish hundreds of wild edible mushrooms, including EMF, because their communities have gathered this food for millennia. Currently, these are frequently very vulnerable social groups with low incomes. Paradoxically, global trade of wild edible mushrooms has recently shown a spectacular increase. According to data from foreign commercial transactions recorded by the United Nations, the volume of wild edible mushrooms has been growing on average around 15% annually over the last decade and has increased more than threefold in the last decade and a half (De Frutos, 2020). De Frutos (2020) reported that, for example, the global trade of fresh or frozen truffles and wild edible mushrooms in 2002 was 181,599 t and by 2017 dramatically increased to 769,162 t, accounting for greater than fourfold increase in 15 years. Similar and maintained trends were found for whole, sliced, powdered, dried and preserved mushrooms and truffles. During the same period, the total global trade of wild edible mushrooms increased more than threefold, from 374,540 to 1,230,124 t. These trends clearly show that there is a global changing demand of consumption habits. If we take into account that a high proportion [e.g., 67% of the 282 edible fungal species commercialized in Europe, Peintner et al., 2013 are mycorrhizal] of the wild edible fungi traded globally are constituted by EMF and the fact that these data do not consider the big unaccountable transaction of EMF commercialized in domestic markets,

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**FIGURE 1** Main genera and their respective percentages in relation to the 970 edible mycorrhizal fungal species known worldwide. Details of bibliographic sources used are provided in Table S1

**FIGURE 2** Main genera and percentage of species of the two most important biocultural centres of edible mycorrhizal fungi (EMF) in the world. (a) China, with 56 ethnic groups and (b) Mexico, with 68 ethnic groups. Sources: Wu et al. (2019) and Pérez-Moreno, Martínez-Reyes, Hernández-Santiago (2020). Currently, 573 and 307 species of EMF are known to be consumed in China and Mexico, respectively. The mycorrhizal status is based on Rinaldi et al. (2008) and Comandini et al. (2012) and the nomenclature follows Index Fungorum (2020)
it is possible to realize the striking global growth of international EMF trade. Healthy and nutritious food has a global open window, as never before, that can benefit the economies of low- and middle-income countries if the EMF trade is conducted in fair and sustainable conditions. Royse et al. (2017) estimated the worldwide annual market value of wild edible mushrooms, most of which are EMF, at US$5 billion.

However, we must consider that the economic issues are just one factor to consider in the sustainable use of EMF, and that one of the biggest challenges currently faced by humankind is how to preserve natural ecosystems, while at the same time feeding a growing human population and increasing incomes in vulnerable human groups. The sustainable use of EMF can be included as part of a worldwide strategy to achieve this goal. EMF are consumed in three scales: (a) self-consumption by rural communities living in areas nearby forests; (b) low-scale commercialization in local or regional markets which constitutes an important proportion of family income during the rainy season for the mushroom gatherers; and (c) international commerce which is worth billions of dollars annually and is an increasing trade industry as mentioned above. In 2015, the member countries of the United Nations signed a 2030 Agenda including 17 Sustainable Development Goals, summarizing the main future global challenges. The use of strategies involving EMF is linked to 11 of 17 UN goals (Figure 3).

3 | THE AMERICAS: A MULTICULTURAL MOSAIC

The current use and history of EMF and their relationships with humans in the American continent is a complex mosaic (Figure 4). It can be divided in three subregions: (a) Canada and the US, (b) Mexico and Central America, and (c) South America. Each area has different sociocultural, economic and environmental singularities.

Canada and US have the greatest economic and scientific development in the Americas. In contrast, the ancient cultural relevance of EMF is fragmented and the records of use of EMF by native groups in this area are scarce. Richards (1997) documented the traditional use as food of species of Tricholoma, Morchella, Ramaria and Lactarius in the Karuk people from western North America, with emphasis on the knowledge of the American matsutake (Tricholoma magnivelarum). Anderson and Lake (2013) summarized the mushroom diversity traditionally used by Indigenous Peoples of California (including Ajumawi, Kashaya, Karuk, and Miwok tribes), including species in the genera Amanita, Boletus, Cantharellus, Craterellus, Hydnum, Morchella, Ramaria and Tricholoma. In contrast with the scarcity of evidence of traditional use of EMF, the scientific development in this area is one of the most copious in the world from the taxonomic, ecological, physiological and "omics" perspectives. Currently, the EMF consumption and gathering is widely distributed and the commercialization of fresh, preserved and industrial products containing EMF has a flourishing market that has been discussed elsewhere (e.g., Pérez-Moreno, Guerin-Laguette, Flores-Arzú, & Yu, 2020). For example, matsutake, porcini, chanterelle and morel markets are a profitable activity.

Mexico and Central America (mainly Guatemala) constitute one of the most important genetic and cultural centres of diversity of EMF worldwide. Mexico is a megadiverse country and a biodiversity hotspot. It has 68 ethnic groups, and it holds one of the largest diversities of EMF in the world, with more than 450 species of wild mushrooms being consumed in the country (Pérez-Moreno, Guerin-Laguette, Flores-Arzú, Yu, et al., 2020). The country has more than 160 species of oaks and 72 taxa of pines, being ranked first place in the world in diversity of these important ectomycorrhizal host trees. The ectomycorrhizal diversity of Mexican ecosystems, including edible species is huge (Garibay-Orijel et al., 2020; Hernández-Santiago et al., 2020). Additionally, there is a pre-Columbian tradition in EMF consumption, as well as self-consumption, commercialization of more than 120 species of EMF sold in local markets, and trading in international markets including US, Canada, Europe and Asia (Pérez-Moreno et al., 2008). In contrast, scientific knowledge is far from complete, and the traditional indigenous knowledge of relevant ethnic groups are only beginning to be studied (Ruan-Soto et al., 2020). For example, the highly mycophilic Nuu savi or Mixtec people [the third most numerous Mexican ethnic group in the country, just after the Nahua (or the so-called Aztecs) and Maya groups], was studied only recently (Hernández-Santiago et al., 2016). Fortunately, currently ethnomycological (see definition of ethnomycology in Box 1) studies are a flourishing research area in the country. Despite its small size, Guatemala constitutes an important cultural centre, mainly of Mayan ethnic groups, and a biodiversity reservoir of ancient knowledge related with EMF (Flores-Arzú, 2020; Mérida Ponce et al., 2019). However, despite its biocultural richness, unique in the world, the development of processed industrial products containing EMF, and important socioeconomical innovations like mycotourism and myco-gastronomy (see Box 1), are only starting.

South America holds a large diversity of EMF, but in the same way as for US and Canada, the ancient records of traditional consumption are fragmentary and scarce. A possible explanation of this conspicuous loss of traditional knowledge is the annihilation made by the Spaniard and Portuguese conquerors of the native south American groups. There was a system called "encomienda" whose main theoretical purpose was to foster European cultural assimilation and conversion to Catholicism of native indigenous people, but in practice led to legally sanctioned forced labour and resource extraction under brutal conditions with a high death rate. According to historian David Stannard, the encomienda was a genocidal system which "... had driven many millions of native peoples in Central and South America to early and agonizing deaths..." (Stannard, 1993). Some recent studies for example, in Chile and Argentina have rescued part of the prevailing mycological knowledge. In these countries there is a range of endemic EMF, mainly in the Patagonian area, associated with Nothofagus forests, that have been traditionally consumed by the Mapuche local native group, previously unreported (Molares et al., 2020). However, in general, studies related to EMF have received little attention in general.
this huge geographical area. A significant exception is the incipient efforts of truffle cultivation in Chile and Argentina. Paradoxically, Mercosur countries (including Argentina, Brazil, Paraguay and Uruguay), Chile and Colombia, for instance, would have potential to export products based on porcini (Boletus sect. Boletus), Suillus spp., chanterelles, Caesar’s mushrooms, morels, and other EMF species, especially by favouring the manufacture of frozen and otherwise preserved products either dried or processed. A good
Figure 4  Mosaic of strategies for the sustainable use of edible mycorrhizal fungi in the Americas. Species with great potential for global trade: (a) Suillus brevipes from Colombia, (b) Amanita jacksonii from Mexico; (c) Ñuu savi girl, belonging to a mycophilic Mesoamerican culture with pre-Columbian knowledge, hunting Caesar’s mushrooms; (d) Laccaria laccata sporome associated with inoculated Pinus montezumae seedling; (e and f) Technology transfer to, and commercialization of preserved mushrooms by tlahuica-pijekakjoo people, who distinguish and consume more than 160 edible fungal species in Central Mexico. Photos: Jesús Pérez Moreno except (c) taken by Faustino Hernández Santiago.
example are *Suillus* species which increase their value after preservation, as their slimy texture results in a short shelf life. This has been taking place for decades, for example between 1980 and 1981, Chile exported more than 2000 t of *Suillus luteus* complex (locally known as *callampas*) with a value of USD$3 million (Pérez-Moreno & Ferrera-Cerrato, 1996). Sitta and Dovoli (2012) reported that the species of the *S. luteus* complex, mainly collected in Chile and Ecuador, are usually sold dried, frozen, or brined rather than fresh. In Argentina, *S. luteus* is consumed mainly fresh and the implementation of mycetourism and mycogastronomy projects have been proposed as new cultural pathways with economic potential (Barroetaveña & Toledo, 2020; Molares et al., 2020). In these scenarios, alliances between rural communities, companies, scientists and local governments are urgently needed in order to boost the sustainable use of EMF in the American continent.

## 4 | EVOLVING MYCOCULTURAL IDENTITY IN EUROPE

Mushrooms have a clear role in defining the cultural identity of a people. While *mycophilic* societies or groups employ an often-vast array of fungal species for multiple uses, especially food, *mycophobic* ones tend to fear fungi, associating them with danger and negative influences. The *mycophobic/mycophilic* divide is not necessarily rigid but rather can be seen as a gradient, especially in modern multicultural societies, yet attitudes towards fungi can still be obviously related to the core cultural composition of a people and to historical human migration events in many instances (Ferreira et al., 2016). Given the complex ethnic composition of Europe and the diversity of human events that has characterized its history, it is not surprising that the use of mushrooms is not uniform across the continent. Roughly speaking, mycophobic areas include the central, northern and north-western countries, while mycophily is common in large parts of southern and eastern Europe, with peaks of "extreme levels of mycophilia" observed in Poland (Kotowski et al., 2019).

However, human culture evolves and what we call traditions can be seen as milestones in a long, adventurous and uninterrupted journey. So, recent ethnomycological research revealed intriguing cases of transition from mycophobia to mycophilia in selected European areas. One such instance is Sardinia, a large island located in the middle of the western Mediterranean basin. Despite being politically part of Italy, a strongly mycophilic country, Sardinians have traditionally shunned using fungi as food, with the exception of a few species. Since a few decades, thanks to increasing contacts and influences from people proceeding from continental Italy, Sardinian society has progressively developed an intense interest for mushroom hunting and consumption (Comandini et al., 2018; Comandini & Rinaldi, 2020). A significant part of the newly prized species is made of ectomycorrhizal fungi, of course, including porcini and other boletes, chanterelles, and milk caps, with local truffles rapidly rising to the status of trendy items (Figure 5a,b). Mycological associations, mushroom exhibitions and an array of handbooks specialized in the rich (and largely unknown) Sardinian mycobiota, are continuously fueling this interest. Sweden is another example of a recent transition from a prevalently mycophobic society to widespread mycophily (Figure 5c). As described by Ingvar Svanberg and Hanna Lindh, the society that gave birth to the founder of modern fungal taxonomy Elias Magnus Fries (1794–1878), did not traditionally consider mushrooms as a suitable food, notwithstanding the abundance of this resource in the country's extensive forests (Svanberg & Lindh, 2019). Starting from the 1830s, Fries and other academic mycologists promoted a sort of "mushroom propaganda", trying to persuade the peasantry about the utility of mushrooms as "emergency food in time of need". Eventually, during the twentieth century, the attitude towards mushrooms progressively changed, and multiple sectors of Swedish society started to be allured by the fungal world. "Swedish society has changed rapidly during the last decades and so has the interest in mushrooming among its members. Throughout the second part of the twentieth century, the flow of information about mushrooms has continued through lectures, courses, media, exhibitions, and even associations," commented the study's authors (Svanberg & Lindh, 2019). "Walking in forestland is also an important leisure activity for many urban Swedes, and in the early twenty-first century, mushrooming has also become a thriving pastime among people with an urban lifestyle" (Svanberg & Lindh, 2019). Within Sweden itself, the Sami make an interesting case for what pertains their view of the fungal world. Living across a large territory stretching from northern Norway, Sweden, and Finland to the Kola Peninsula in Russia, some 80,000 Sami (20,000 in Sweden) strive to defend their indigenous culture despite the inevitable pressure to change their way of life (https://sweden.se/society/sami-in-sweden/#). The available accounts show that even among the Sami the attitude towards fungi is not uniform and has been probably shaped by a complex mix of environmental and cultural factors. While the Sami in Finland and Russia are known to commonly consume mushrooms as food, people in the rest of northern Fennoscandia have generally not considered mushrooms as a suitable food resource, if not in very special cases (Inga, 2007; Svanberg, 2018) the scented bracket fungus *Haploporus odorus* (Sommerf.) Bondartsev & Singer has been utilized by Sami and Swedish peasants in northern Sweden as a seasoning in cheese and bread, and other polyopes have been used to make teas or infusions (Svanberg, 2018). Much more widespread was the use of several fungal species, especially bracket fungi, for purposes other than food. Indeed, the Sami largely utilized polyopes for fire-making and tinder, in folk therapy, as repellents, as perfumes, and even as toys (DuBois & Lang, 2013; Svanberg & Lidström, 2019).

## 5 | AFRICA: THE CONTRASTING NORTHERN AND THE SUB-SAHARAN AREAS

Northern Africa is traditionally inhabited by Berbers and Arab people, which contrasts with the ethnic groups inhabiting Sub-Saharan area in the Central and Southern part of the continent. The vegetation types that hold EMF in Northern Africa include the Mediterranean, steppe and desert climatic zones. These areas harbour pine, oak and
cedar forests where morels, boletes, Caesar’s mushroom, Ramaria, matsutake [Tricholoma nauseosum (A. Blytt) Kytöv. = T. matsutake (S. Ito & S. Imai) Singer] and truffle (Tuber spp.) species have been traditionally consumed and used as medicine. In steppe and dry areas, desert truffles belonging to the genera Delastria, Terfezia, Tirmania and Picoa, usually associated with shrubs and grasses belonging to the genera Cistus and Helianthemum, have been traditionally harvested, commercialized and consumed by native groups, and known as tirfas in the Berber language, and in Algeria, Morocco and Tunisia as terfess in Arabic language. Commanding a much lower price than true truffles, these desert truffles have been traded from Northern Africa since Roman times (Khabar, 2016). They were highly valued by Greeks and Romans. For example, the Roman poet Juvenal in the early 2nd century wrote in his Satire 5, "... Then will be served up truffles, if it happens to be spring ... devoutly wished for by the epicure, shall augment the supper. "Keep your corn, O Libya," says Alledius, "unyoke your oxen; provided only you send us truffles!..." (Juvenal, 1885).

A contrasting biocultural situation exists in sub-Saharan Africa with hundreds of cultures and more than one thousand native languages, which constitute one of the largest ethnic diversities in the world. Although Africa is the second largest continent, the area covered with forests and hence the area that is potential home for EMF is lower compared to Europe and the Americas: 675 million hectares (according to U.N, FAO). But there are few places on Earth where the close connection between people, forests and mushrooms is as visible as it is in Africa’s woodlands. Rural populations living in and around the forests are particularly dependent on many of the forest products and ecosystem services, not least edible fungi. You will encounter a colourful and tasty variety of species offered for sale along the roads, in villages and in markets mainly by women and children. These mushrooms, amongst which many are ectomycorrhizal, are one of the more important renewable natural resources, especially at the beginning of the rainy season which is the traditional hunger period (Boa, 2004; Rammeloo & Walleyn, 1993). Mushrooms are
eaten fresh, dried or cooked. The five main genera consumed by local people are *Amanita*, *Cantharellus* (Figure 6a), *Russula* and *Lactifluus* which are ectomycorrhizal, and *Termitomyces* which has a symbiotic relationship with termites. Since the primary forests are cleared at a rate of 4 million hectares each year, awareness of the close association between trees and their ectomycorrhizal fungi is needed for sustainable forest management and restoration. Knowledge is the key to protection and conservation. Though the traditional knowledge is impressive in many areas, solid mycological studies in Africa were scarce compared to most other continents. Reasons for this are the lack of training and mycologists, inadequate structure and hard-to-reach areas, and not the least: a huge diversity that is almost completely endemic and cannot be assessed with European identification tools.

But the times are changing! Mycological studies exploring the African mycodiversity are increasing fast, resulting in the description of many new species, up-to-date classification tools (Buyck et al., 2013, https://www.ffta-online.org/), a website on edible fungi of tropical Africa (https://www.efta-online.org/) and several books focusing on edible species in different areas (Degreef & De Kesel, 2017; De Kesel et al., 2002, 2017; Härkönen et al., 2003). In 2019, the First African Symposium for Tropical African Mycology was organized in Benin and brought together the scientific curiosity, experience and expertise of more than 80 mycologists from 24 different countries, most of them are African (Figure 6b). Concern for ecosystems and the search for sustainable management was an omnipresent theme.

Ectomycorrhizal trees and their fungal partners are dominant in the woodland associations: Zambezian miombo woodlands in southern to central and eastern Africa constitute the most extensive vegetation type in Africa, dominated by trees of the leguminous genera *Brachystegia*, *Julbernardia* and *Isoberlinia*, all ectomycorrhizal. The Sudanian woodlands lack *Brachystegia* and *Julbernardia* species, but are rich in *Isoberlinia*, *Burkea*, *Afzelia* (Caesalpinaceae) and *Uapaca* (Euphorbiaceae).

More humid forest types (Guineo-Congolian rainforest, riparian forest, gallery forest, dry evergreen forest, etc.; vegetation types according to White, 1983) have local patches of monodominant trees such as *Gilbertiodendron* (Caesalpiniaceae) or local dominance of *Uapaca* species. Many ectomycorrhizal mushroom species have a high ecological selection and a preference for either woodlands or rainforest types. Some seem to be restricted to a particular type of woodland or forest, others seem less selective and occur both in woodland and forest vegetation. Local research projects for inventories, red lists and protection programs have been launched in several countries, especially in West-Africa (e.g. Houdanon et al., 2019; Kamou et al., 2017;
Léabo et al., 2017). ECM symbioses play an important ecological role, which is a response to the soil conditions - often poor in organic content, especially in the woodlands - and they are indispensable for the dominant trees. Additionally, they have other relevant ecological functions in the ecosystems, for example they constitute an important player in food chains (Ayer & Egli, 1991; Claridge et al., 1996; Currah et al., 2000). There are few studies in Africa about relations between animals and fungi, and their importance is underestimated. But one of the striking examples is the tortoise genus *Kinixys*. Although omnivorous, *Kinixys spekii* has a diet that consists of 40% mushrooms (Hailey et al., 1997, 1998). Primates such as gorillas, chimpanzees and vervet monkeys have been observed to consume sporomes on different occasions (Verbeken, pers. comm.). And everyone who collects mushrooms in tropical Africa will have experienced the giant millipedes as competitors, hiding in— and hollowing out the most beautiful, fleshy specimen. Apart from the many roles they fulfil for the people and the environment, African ECM fungi are also indispensable to answer evolutionary questions world-wide. As mentioned before, most African ECM species are endemic to the continent, some even represent unique African infrageneric groups. We need the knowledge of the diversity in this continent to make the story complete. Up to date phylogenies of ECM taxa include a growing amount of data from traditionally underexplored areas and hence help us to understand the evolutionary history. For the Russulaceae family, the largest genus *Russula* is supposed to have a Northern hemisphere origin (Buyck et al., 2020). *Lactifluus* is mainly a tropical, diverse ECM genus, for which an African origin, followed by a spread to different continents, is hypothesized (De Crop, 2016; De Crop et al., 2017). And for *Lactarius*, we also hypothesize a tropical African origin followed by a diversification in the Northern Hemisphere in a variety of ecosystems. Understanding this evolution as a function of climate and available host trees, offers the key to solid protection and regeneration.

**6 | ASIA AND THE ICONIC CASE OF CHINA**

EMF are critical components of forest ecological systems, highly diverse, and important in subsistence and market-based livelihoods worldwide (Boa, 2004; Cunningham & Yang, 2011). One of the most iconic examples of this statement is appreciated in Southern Asia, particularly in China. This country holds the world’s richest diversity of wild edible mushrooms, with over 800 edible species recorded (Wang & Yang, 2006), and around 75% of these species distributed in Southwestern China. At the main markets such as those in Kunming and Nanhua, hundreds of tons of wild edible mushrooms change hands daily during mushroom season from June to October (Figure 7a). Over 320 species, belonging to 101 genera, and 47 families have been reported to be traded in the local markets (Dai et al., 2010; Wang & Liu, 2002; Wang et al., 2004; Yu & Liu, 2005). Of these edible mushrooms, about 250 species are associated with Pinaceae, Fagaceae, Betulaceae and other forest-dominating tree species establishing ECM symbioses. More than 164 species are commonly traded and 60 dominant commercial species, including mainly the EMF genera *Boletus*, *Cantharellus*, *Lactarius*, *Lactifluus*, *Ramaria*, *Russula*, *Thelephora*, *Tricholoma* and *Tuber*, have been reported from Yunnan’s local markets (Figure 7; Wang et al., 2004). In China, wild edible mushrooms can be consumed as food or medicine, but can also provide a source of extra income (Zhu et al., 2019). The foreign income produced from wild edible mushroom exportation is over USD$ 100 million every year in China. Marketing of *T. matsutake* (Figure 7c), and a few additional species, such as the *Tuber indicum* complex (Figure 7d) and *Boletus bainiugan* has significantly improved the local economy throughout the Hengduan mountainous area (Wang & Yang, 2006). Harvesting of edible mushrooms is an important livelihood and generates 15%–90% of these people’s annual income. Currently, there are about 15 million farmers working with wild edible mushrooms, and more than 400 factories process them, generating more than 20 million jobs directly working in this industry (Liu et al., 2018; Figure 7e). For instance, in the last 10 years, over 1,000 t of fresh fruiting bodies of matsutake have been exported from Southwestern China annually. More than 40 counties in Yunnan are reported to harvest matsutake (Yang et al., 2009). In Shangri-La county, northwest Yunnan, matsutake accounted for 50%–80% of rural household income (Yang et al., 2008, 2009; Figure 7c).

However, the intensive and continual harvest of fungal fruiting bodies at an unprecedented scale for the international and domestic markets has had severe impacts on EMF abundance and their associated habitats. The natural production of some high-priced EMF such as matsutake, truffles and *Thelephora ganbajun* has declined since large-scale commercial harvesting initiated in the 1990s (Hua et al., 2017; Liu et al., 2018). Conservation of this precious biocultural resource remains a vital and urgent issue. Great efforts were encouraged to use EMF in a sustainable way in order to promote rural development (Brown et al., 2018; Geng et al., 2009; Wang, Guerin-Laguee, Butler et al., 2019; Wang, Guerin-Laguee, Huang et al., 2019), including (a) improvement of public awareness for environmental protection and sustainable development, (b) development of EMF cultivation to improve quality and supply and reduce harvest pressure, and (c) promotion of mycotourism and development of mushroom gastronomy in rural agro- and slow-food tourism (Liu et al., 2018). However, the most important action has been the forest ownership reformation which occurred in 2008, giving farmers the right to manage forest products including wild mushrooms. A few regulations have been launched such as prohibiting the harvesting of immature matsutake and truffle sporomes, collecting with proper tools and rehabilitating the habitat after harvesting. A few reserves for protection and study of matsutake, truffles and *T. ganbajun* have already been established and more are planned (Huang et al., 2011; Qu et al., 2010). Experimental plantations have been set up for Chinese truffle (*Tuber indicum*) cultivation, and production has already begun in some of them. Additional attempts to cultivate and to understand the basic ecological and biological principles of other truffle species (*T. borchii*, *T. huidongense*, *T. liyuanum*, *T. melanosporum*, *T. panzhihuanense*, *T. pseudohimalayense* and *T. sinoestivum*).
and milk cap mushrooms (L. akahatsu, L. deliciosus, L. hatsutake and L. vividus) have also started (Deng et al. 2014; Geng et al. 2009; Huang et al., 2020; Wan et al. 2016; Wang, Guerin-Laguette, Butler et al., 2019; Wang, Guerin-Laguette, Huang, 2019; Wang et al., 2020).

7 | AUSTRALASIA: THE UNIQUENESS CASE OF NEW ZEALAND

In a recently published book chapter (Pérez-Moreno, Guerin-Laguette, Flores-Arzú, & Yu, 2020), we presented the unique characteristics of New Zealand both from a natural point of view (a country that has been isolated from the rest of the world for 80 million years) and a cultural point of view (a country that has been colonized only very recently by humans: mainly Māori then European people for <800 years). These characteristics have strong implications on edible fungi, native or exotic, mycorrhizal or saprotrophic. In the present contribution, we present in more detail the potential offered by EMF in New Zealand, highlighting achievements to date in terms of their cultivation and use, and presenting future opportunities focusing on both exotic and native EMF species.

New Zealand is well-known for having pioneered the cultivation of several EMF species. New Zealand made history when it cultivated the Périgord black truffle (Tuber melanosporum Vittad.) for the first time in the southern hemisphere in Gisborne in 1993 (Guerin-Laguette, 2008; Wang & Hall, 2004), being only second to the United States to cultivate this species outside of Europe. After several other cultivation successes from out-planted mycorrhized seedlings [Tuber borchii Vittad. (bianchetto), Tuber aestivum (Wulfen)]
Spreng. (Burgundy truffle) (Guerin-Laguette, 2008), *Rhizopogon roseolus* (Corda) Th. Fr. (shoro) (Visnovsky et al., 2010), New Zealand has been considerably advancing the cultivation of *Lactarius deliciosus* (L.) Gray (saffron milk cap) in pine orchards and demonstrating its full potential in terms of yields (Figure 8a–c; Guerin-Laguette et al., 2014, 2020, 2021). The quantity of cultivated truffles is now exceeding 1 t per annum with production increasing every year. *Tuber melanosporum* and *T. borchii* are the main truffle species cultivated in New Zealand (Figure 8d–h). A new industry is emerging (https://www.nztruffles.org.nz/) and shows promise of growth as growers now consider exporting truffles and taking shares of the large international truffle market.

The first application of EMF cultivation skills could be directed to the establishment of intensive truffle and mushroom orchards. Although considerable applied research is still required to understand and optimize EMF yields (Guerin-Laguette, 2021), this field holds great promise for New Zealand as an innovative/complementary approach to use arable or marginal land in New Zealand regions already dedicated to the cropping of exotic species in the agricultural, horticultural and forestry sectors. Indeed, sustainable EMF orchards offer several

![Figure 8: Edible mycorrhizal fungi in Christchurch, New Zealand.](image-url)

(a) *Lactarius deliciosus*: (a and b) cultivated basidiomata; (c) ectomycorrhizae, bar 500 µm; (d–f) *Tuber melanosporum*: (d and e) cultivated ascomata; (f) ectomycorrhizae with *Quercus ilex*, bar 660 µm; (g and h) *Tuber borchii*: (g) large (182 g) cultivated ascoma; (h) ectomycorrhizae, bar 400 µm; (i and j) *Boletus edulis*, one of the most popular edible ectomycorrhizal mushrooms in the world known usually as “porcini”, not yet cultivated but thriving naturally in Canterbury after its accidental introduction to New Zealand: (a) basidioma; (b) ectomycorrhizae, bar 250 µm. Photos: Alexis Guerin-Laguette except (d) and (e) taken by Wayne Tewnion.
benefits such as: (a) a contribution to mitigate the effects of climate change by increasing carbon storage in the trees and in the soil; (b) a premium food product that can generate a value chain based on gourmet fungi, including their health benefits; (c) a logical inclusion of EMF to agroforestry or edible forests and a further incentive to support innovative farming approaches (regenerative agriculture and a multi-cropping system that could include edible nuts produced by host trees: hazelnut, stone pine, chestnut); and (d) a habitat for wildlife, including potential predators of insect pests impacting agricultural fields surrounding the orchards and a shelter for animals.

The second application could come from the development of low-cost, large-scale inoculation techniques of EMF for their use in mass production of forestry seedlings. Currently efficient, low-cost, large-scale inoculation techniques are lacking for most valuable EMF species such as saffron milk cap, porcini, matsutake or Japanese shoro (see Box 1). Forestry entrepreneurs are often conservative and not always prepared to incorporate changes in forestry practices to accommodate for the fungal crops, including for example different tree spacing, pruning or branch removal. Mushroom conservation and processing also has to be improved to develop ‘value add’ products that could increase shelf life and create an economic return justifying investment and change of practices. Indeed, New Zealand has vast available land, especially if cattle farming is reduced, and a strong forestry sector that could increase the value of planted forests by introducing EMF and generating yearly income from their harvest and processing while capitalizing on the benefits they provide to tree growth and resilience.

Other high value exotic EMF species considered present in New Zealand have yet to be mastered in terms of cultivation, i.e., *Tuber magnatum* Picco (Alba truffle), *Tricholoma matsutake* (S. Ito & S. Imai) Singer (matsutake) and *Boletus edulis* Bull. (porcini). The former two species are not currently growing in the wild in New Zealand but can be researched for cultivation purposes, i.e., there are no biosecurity restrictions to grow them from pure authenticated material. *Boletus edulis*, however, is fruiting naturally and thriving in some areas such as Canterbury (Figure 8i-j; Guerin-Laguette et al., 2011). Should scientists discover an efficient method to propagate and cultivate *B. edulis*, this would provide a significant economic benefit to New Zealand given *B. edulis’s* wide range of host trees, the large international market for this species, and the multitude of value-added products that can be derived from the sporomes (for example, dried porcini mushrooms as an ingredient of culinary products). New Zealand’s native beech forests (*Nothofagus* Blume, subgenera *Fuscospora* and *Lophozonia*) host a wide range of ectomycorrhizal fungi (*Orlovich & Cairney, 2004*). Unlike northern hemisphere countries, knowledge regarding the edibility of beech-associated ectomycorrhizal fungi is lacking. However, combined phylogenetic and biochemical studies could likely identify species with edible or medicinal properties. This would open new opportunities for the sustainable use, or cultivation, of native EMF species associated with these iconic New Zealand trees.

Māori have strong spiritual bonds to their mother land, Papatūānuku (the Earth Mother). The sustainable use and farming of EMF, native or exotic to New Zealand, corresponds to the Māori ancestral vision of protecting and enhancing the land through its appropriate use (Evison, 1997). Furthermore, EMF offer an opportunity for Māori to engage in the science of mycorrhizal symbiosis, a fascinating plant/fungus interaction underpinning the development of their multiple applications. Knowledge of Māori usage of mushrooms is largely limited to records by early European writers who recorded what they observed (Fuller et al., 2004). Māori themselves passed knowledge down orally between generations but sadly most of this has been lost: few Māori today are aware of fungi (hekaheka) that were important to their ancestors (Buchanan, pers. comm.). The development of the outdoor cultivation of EMF in New Zealand would increase awareness for wild edible fungi, native or exotic, including culturally important wood-inhabiting native species such as *Hericium novae-zealandiae* (Colenso) Chr.A. Sm. & J.A. Cooper or *Cyclopye parasitica* (G. Stev.) Vizzini (Buchanan et al., 2017; Chen et al., 2020). EMF cultivation would complement recent efforts on cultivation research of these two species and of hitherto poorly known species of potential great significance, for example *Lentinula novae-zealandiae* (G. Stev.) Pegler, a shitake-relative endemic to New Zealand (Johnston, 2010; Buchanan P, pers. Comm.). With recent advances in biotechnologies and our increased capacity to manipulate and better understand the interactions between trees and their fungal mycorrhizal partners, the applications of EMF for the benefit of New Zealand and its people are countless and await a bright future. For example, some local companies run by scientists are currently aiming at providing advice and services based on knowledge and experience that could help landowners to establish successful EMF orchards (http://www.mycotree.co.nz).

**8 | GLOBAL CHALLENGES, PERSPECTIVES, CONTRIBUTION FOR HUMAN WELL-BEING AND NATURE CONSERVATION**

The main challenges and perspectives in the sustainable use of EMF can be summarized in the following points:

(i) A big challenge is to boost the establishment of successful EMF orchards around the world (Guerin-Laguette, 2021);

(ii) Climate change has dramatically impacted the rainfall patterns or the proliferation of some forest plagues and diseases mainly in stressed trees, and, as a consequence, a number of species, including matsutake, and truffles have declined (Borunda, 2019; Büntgen et al., 2019; Faier, 2011; Guo et al., 2017). Therefore, a priority is the development and application of forest management techniques, including cultivation, to enhance EMF production, which has been named mycosylviculture (see Box 1);

(iii) Actions to mitigate climate change, including successful reforestation using EMF as bio-inoculants of native trees, constitute an urgent need (for example in Mexico more than 130 combinations of native trees and EMF have been tested, using inoculation techniques which are simple, efficient and have a low cost). With the use of these techniques, a conspicuous
enhancement of plant growth, nutrient contents, physiological quality and survival of planted seedlings under field conditions have previously been demonstrated (Pérez-Moreno, Martínez-Reyes, Hernández-Santiago, & Ortiz-Lopez, 2020);

(iv) Non-sustainable harvest techniques have dramatically reduced the natural production of many EMF world-wide (Borunda, 2019; Büntgen et al., 2019; Ehlers & Hobby, 2010; Mortimer et al., 2012). Therefore, environmental education of the native gatherers by scientists with the support of local governments or NGO’s needs urgent attention. Along with this, national or regional certification of sustainably collected EMF; which is currently lacking, is also necessary;

(v) Technological transfer of processes that provide an added value to EMF, by using a range of simple to industrial preservation processes or EMF products according to the species, by scientists or technicians mainly in low-income countries are necessary;

(vi) The promotion of a fair trade with local and regional rural communities living in nearby the forests (through the creation of local cooperatives, involving mainly women), would promote the sustainable use of EMF (and at the same time would contribute to women empowerment) and poverty alleviation in socially marginalized, low-income and vulnerable groups;

(vii) Promotion of innovations including mycotourism and mycogastronomy establishing fair alliances between social groups, entrepreneurs, scientists and local governments are needed. This would boost economic development in rural communities by creating local jobs involved in mycological trails, rural lodging, sale of local mycological products, and consumption of EMF in local restaurants. Currently, this activity is already seen in several areas of Canada, US, Mexico, Chile, Portugal, Spain, France, Scotland, Italy, Macedonia and South Africa (Jiménez-Ruíz et al., 2017; Martínez-Peña et al., 2011);

(viii) Creation of government channels to promote the domestic and international commerce of preserved EMF or EMF-based products, with strict food safety and quality control regulations, would allow poverty mitigation and creation of jobs; and

(ix) Promotion of the relevance of EMF biocultural heritage (in ancient mycophilic cultures around the world, whose knowledge of this relevant genetic resource has been generated during thousands of years), would allow the development of sustainable commercial activities involving EMF. This would also promote the cultural identity and the preservation of native languages (and multiworld-visions) of ethnic groups that currently are at high risk of extinction due to rapid acculturation processes which are happening at a speed never seen before in human history.

Sustainable use of EMF would allow both the preservation of forests including the preservation of their biodiversity, and rural development, with their environmental, economic and socio-cultural implications. Additionally, biotechnological applications of inoculants based on EMF would allow mycoremediation of contaminated areas and successful reforestations and forest plantations with the consequent mitigation of global change, through the reduction of greenhouse gases emission to the atmosphere. In summary, the perspectives of the sustainable use of EMF, contributing to environmental protection, economic development, protection of biocultural heritage created during millennia in many cultures around the world, and development of fair trade is not only possible but an urgent need in the current world, particularly, in the hard social, economic, and environmental challenges that we will face around the world in the post-pandemic era that we will live in near future.

9 | CONCLUSION

It has been widely documented that the emergence of zoonosis is related with a disequilibrium between the relationships of humans and nature, including wide deforestation and invasion of domestic animals for food production in natural ecosystems (Dobson et al., 2020; Jones et al., 2008; Kenyon, 2020). Health, environmental and economic crisis are interwoven worldwide. Thus, in the current postpandemia COVID-19 scenario, the development and application of technological innovations whose inspiration is the creation of a new relationship and models between nature and societies are necessary. These should take into account local knowledge of communities and indigenous cultures, which have remained marginally included in ecosystem management plans, and are now strategic to mitigate the global environmental and economic crisis that we live and will continue to face in the near future worldwide. The sustainable use of EMF around the world, in countries and areas that have this potential should be boosted, looking for an equilibrium of a sustainable use of this relevant genetic resource between their rational use and the preservation of the forested areas where they thrive. In this scenario, it is important to consider that the situation in different regional areas in different continents is a mosaic due to the range of historical, cultural, social, environmental, geographical, economic and political situations, generating diverse challenges and perspectives around the world. Therefore, the strategies related to EMF to be applied in each particular context have to take into account these differences.

ACKNOWLEDGEMENTS

This article is dedicated to the British Professor Sir David Read for his valuable contributions to the study of mycorrhizal symbioses and to the Chinese Dr. Wang Yun for his original studies related to the field of edible mycorrhizal fungi. Both of them have inspired the development and application of these scientific fields around the world. Funding from the Mexican Council of Science and Technology (CONACyT) through a sabbatical stay in China to JPM is acknowledged. International (Regional) Cooperation and Exchange Projects of the National Natural Science Foundation of China (No. 31961143010), Open-Funds of Scientific Research Programs of
State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau (A314021402-2002) is also acknowledged. We deeply thank the handling editor and two anonymous reviewers for their constructive comments, which helped us to improve the manuscript. Permission provided by those featured in the photographs are also acknowledged.

AUTHOR CONTRIBUTIONS

JPM and FQY conceived the manuscript; JPM, AG-L, ACR, FQY and AV wrote the paper; FHS and MMM conducted the data analysis. All authors reviewed and approved the final version.

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SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Pérez-Moreno J, Guerin-Laguette A, Rinaldi AC, et al. Edible mycorrhizal fungi of the world: What is their role in forest sustainability, food security, biocultural conservation and climate change? *Plants, People, Planet*. 2021:00:1–20. https://doi.org/10.1002/ppp3.10199