Chapter 1
Setting the Scene

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1.1 Believe It or Not

For many people, the word 'mushroom' is immediately associated with the cultivated button mushroom, known technically as *Agaricus bisporus*. However, mushrooms are of course much more diverse than this single species. Just to give an example, if we type the word 'mushroom' in the Google search bar, 289 million entries will appear. According to the Encyclopaedia Britannica (2019) mushrooms are defined as 'the conspicuous umbrella-shaped fruiting body (sporophore) of certain fungi, typically of the order Agaricales in the phylum Basidiomycota but also of some other groups'. Mushrooms are indeed the spore forming structures of a very large group of living organisms which form a kingdom of their own, the fungi. They constitute an important structural and functional component of the earth ecosystems. The world would not be able to exist as we know it, without fungi. Saprotrophic fungi are responsible for breaking down dead plants, animals, and microbes and recycling the nutrients contained in them, hence bringing them back in the cycle of life. We can say that fungi are the greatest disassemblers of complex compounds in

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J. Pérez-Moreno et al. (eds.), *Mushrooms, Humans and Nature in a Changing World*, https://doi.org/10.1007/978-3-030-37378-8_1

nature. Unlike plants or animals, the body of an individual fungus is hidden underground or in the substrate and is not composed of cells but of networks of filaments (called hyphae individually and mycelium as a whole).

Since their appearance in evolution history, fungi have played a key role in the structure and functioning of natural ecosystems. Fungi not only have adapted themselves to colonize all of the earth's environments but also have contributed to shape them as we know them currently. Let's present just two iconic examples of how these dynamic processes involving fungi have been at play. First, there was a time in the geological history of the earth when life was at risk due to the accumulation of plant debris made up of lignocellulose polymeric compounds and when swamp forests locked up the global atmospheric CO_2. The accumulation of such substrates was enormous and there was no natural process to break them down efficiently. A genetic mutation in a group of fungi (Basidiomycota) empowered them to produce the proper group of enzymes, known as ligninolytic peroxidases, allowing the degradation of polymeric compounds and solving once for good this fundamental problem for life. Since then, a particular group of saprotrophic fungi, particularly belonging to Basidiomycota and mostly mushroom-forming, are responsible for nutrient cycling by degrading very complex polymers such as lignin and celluloses. Those that break down lignin first are the so-called white rotters; those that start degrading the wood by breaking down the celluloses are the brown rotters. In order to elucidate which group of Basidiomycota was involved and to determine the geological period during which this mutation happened, a number of studies have been carried out. Mushroom genomes have been of paramount importance to study the enzyme groups that have the ability to carry out white and brown rots. Indeed, genomes provided an understanding of the mushrooms evolutionary timeline and more accurate timestamps for when Basidiomycota groups might have developed the ability to break down all woody components in plant cell walls. First, it was discovered that the evolution of white rot fungi around 300 million years ago coincided with the end of the coal forming Carboniferous period, impacting the global carbon cycle (Floudas et al. 2012). Later on, it was demonstrated that additional to peroxidases, other enzymes, including those that attack crystalline celluloses, also contributed to the decomposition of polymeric compounds of woody plant cell walls, widening the understanding of the origins of lignin-degrading fungal enzymes (Nagy et al. 2016). More recently, it has been shown that a powerful evolutionary convergence process also existed, and that peroxidases of Polyporales (an important group of wood-decaying Basidiomycota often forming tough and striking mushrooms—also called bracket fungi) acquired the ability to degrade non-phenolic lignin using a tryptophanyl radical interacting with the bulky polymer at the surface of the enzyme (Ayuso-Fernández et al. 2018). It is currently accepted that Basidiomycota mushrooms were the pioneer lignocellulosic decomposers through different evolutionary mechanisms during the Paleozoic era. These mechanisms were keystone evolutionary processes, which modified the whole earth ecosystem structure and function, contributing to shape the world as we currently know it.

A second iconic example is related to the influence of fungi as rain-makers, a fascinating illustration of their influence on life on earth. We know that rain stimulates mushroom growth, however, it has also been discovered that on the other way around, mushroom spores (including species of *Lactarius*, *Suillus*, *Russula* and *Lycoperdon*) act as condensation nuclei, which means that they have surfaces on which water vapour condenses in order to form big water droplets which eventually will produce rain (Hassett et al. 2015). The mechanism starts when the spores secrete mannitol and other water-loving sugars that trigger the formation of a tiny ball of water around individual spores. Interestingly, these carbohydrates are present during the spore discharge but they evaporate once the spore is airborne. Thus, the liquid water modifies the fluid motion and results in a rapid displacement of the spores' centre of mass, imparting momentum and launching it skyward at up to 6.5 km/h (Stolze-Rybczynski et al. 2009). Due to the large number of spores released by mushrooms, this process has a global influence. A single mushroom can release around 30,000 spores every second, and then billions can be produced per day (Money 2011). It has been estimated that globally 50 million tons of mushroom spores are dispersed into the atmosphere each year (Elbert et al. 2007). The global influence of this phenomenon is simply impressive because it implies that those tiny spores produced by mushrooms, influence rain formation and therefore have driven climate patterns around the globe, from rainforests to boreal forests since long ago.

Besides the saprotrophs, another important trophic group of fungi, is composed by those who damage plants, animals, or other microorganisms and live as parasites. It would be surprising to know that in terms of size, the largest organism on earth is a mycelial mat (or body) of the opportunistic parasite edible mushroom *Armillaria ostoyae*, known as Humongous fungus, which covers 965 ha, with a maximum length of 3.8 km and an estimated age of 8500 years. This giant genet (the equivalent designation of individuals for fungi) is located in the Blue Mountains of Oregon, the United States. This fungal genet has a huge mycelium that permeates below the forest floor and parasitizes hundreds of trees. To confirm the size of this organism, molecular analyses called restriction fragment length polymorphism (RFLP) and rapid amplified polymorphic DNA (RAPD) were used. The mushrooms formed by this mycelium appear above ground about once a year, around the base of infected or newly killed trees. Theoretically, this organism may continue growing indefinitely (Ferguson et al. 2003). Paradoxically, this organism grew undetected during millennia until the beginning of the twenty-first century. In other species, it is not as much the mycelium, but rather the mushrooms that can be very big and heavy. The largest and heaviest mushroom is a perennial giant polypore, *Phellinus ellipsoideus*, found in Hainan Island in southern China, where it lives as a saprotrophic species. When it was discovered in 2012, it was 20 years old with an estimated volume of 500,000 cm^3, a length of 10 m, a weight of half a ton and it had around 452 million pores, which might produce 1 trillion spores per day (Dai and Cui 2011). Interestingly, anti-tumor bioactive compounds against liver cancer have been isolated from this mushroom (Zan et al. 2012).

The third trophic group of fungi is probably the most fascinating from both a structural and functional perspectives in natural ecosystems. This group also forms the mushrooms that are the starring players in this book: edible mycorrhizal fungi. The mycorrhizal symbiosis is established between the roots of 90% of plants and thousands of fungal species. This symbiosis played a key role in the colonization of land by plants. The oldest fossil records have been found during the Ordovician and Devonian periods, 460 and 407 million years ago, respectively (Remy et al. 1994; Redecker et al. 2000). The colonization of the earth by plants, and the subsequent development of life on the terrestrial surface, was driven by this symbiosis (Pirozynski and Dalpé 1989; Taylor and Osborn 1996; Brundrett 2002). In the mycorrhizal symbiosis, plants and fungi are in close contact in order to exchange nutrients. Around 10–20% of the carbohydrates photosynthesized by the plants are transferred to the mycorrhizal symbionts, and in return, the fungi transfer macro- and micronutrients and water to their associated host plants, conferring them resistance to stress originated by pathogens, potentially toxic elements, and drought (Smith and Read 2008). Particularly one type of mycorrhiza, called ectomycorrhiza, whose origin dates back to the Cretaceous period is currently established between around 8500 gymnosperm and angiosperm plant species (Brundrett and Tedersoo 2018) and more than 20,000 mushroom species (Comandini et al. 2012). It is possible to state that without this symbiosis, there would be no forests, particularly in boreal, temperate, and some subtropical and tropical areas. Very recently, by analysing over 1.1 million forest plots globally distributed, Steidinger et al. (2019) estimated that ectomycorrhizal trees constitute approximately 60% of tree stems on earth. This symbiosis dominates forests where seasonally cold and dry climates inhibit decomposition, located at high latitudes and altitudes. The authors of this research named this effect 'the Read's Rule' after the British pioneer scientist working on symbiosis, Sir David Read from the University of Sheffield, who first predicted this distribution almost three decades ago (Read 1991). It has been demonstrated that ectomycorrhizal fungi tend to increase the amount of C stored in soil (Averill and Hawkes 2016) and that these types of mushrooms have the ability to modify their local environment to further reduce decomposition rates by mineralizing forest organic compounds (Read and Pérez-Moreno 2003). Through this global model, Steidinger et al. (2019) have predicted massive changes in the symbiotic state of the world's forests that will be linked to strong modifications of the global climate if C emissions continue being unabated by 2070. Another fascinating discovery is that through the connection of different plants and mycelia, very complex networks connect trees in nature (Pérez-Moreno and Read 2004). Through these networks, nutrients, water, and signal compounds are transferred between trees. For this reason, these mycelial networks have been called the 'wood wide web'.

The fruiting bodies of some ectomycorrhizal fungi are edible, and this specific sub-group is the main subject of this book: edible ectomycorrhizal mushrooms, or EEMs. The international commerce of EEMs is worth billions of US dollars annually (Yun and Hall 2004). Additionally, hundreds of bioactive compounds with analgesic, anti-allergic, anti-carcinogenic, anti-bacterial, anti-coagulant, anti-fungal, anti-hypertensive, anti-inflammatory, anti-nociceptive, anti-oxidant, anti-pyretic, anti-venom, anti-viral (including anti-HIV), cholesterol-lowering, hepatoprotective, and with immune enhancement properties have been isolated from more than 100 species of EEMs (Pérez-Moreno and Martínez-Reyes 2014). However, the study of this important group of mushrooms is still in its infancy. Vast mycological diversities of ectomycorrhizal mushrooms around the world have been poorly studied or not studied at all. The inspiration of this book is to encourage studying this important group of mushrooms from the ecological, social, cultural, and economic points of view.

1.2 Early Interactions

In addition to their ecophysiological relevance, mushrooms have played an important role in the development of human civilizations as we know them currently. In different cultures around the world, they have been ancestrally used as food, flavouring, medicine, and sacred elements. Deadly or poisonous species often represent death or disease. More recently, it has been shown that they are the source of bioactive compounds with applications in industrial processes related with the enzyme production of stains, cosmetics, biopesticides, and bioactive compounds with a wide range of uses. The most ancient evidence of mushroom consumption by humans dates back to the Stone Age. An international team led by Robert Power of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, discovered that in the Upper Palaeolithic, humans already ate a variety of plants and mushrooms. They identified spores of Agaricales and Boletales (specifically boletes) in a tooth plaque of an old woman dated 18,700 years old by radiocarbon techniques, found at El Miron cave, Cantabria, in northern Spain (Power et al. 2015). Additionally, the ancestral uses of *Amanita muscaria* (commonly known as the fly agaric) in Siberia, and of *Psilocybe* spp. (known as *teonanácatl* in Aztec language meaning the God's flesh) in sacred ceremonies in Mexico have been subject to a vast body of literature (e.g. Wasson and Wasson 1957; Wasson 1980; Riedlinger 1990). *A. muscaria* was widely used as an entheogen by many of the indigenous peoples of Siberia (Saar 1991b). Ostyak and Vogul tribes in western Siberia and Kamchadal, Koryak, Chukchi tribes in eastern Siberia still use *A. muscaria* for shamanistic rites. The isoxazoles, especially muscimol, pass through the human renal system almost intact, and thus it is possible to ingest them by drinking human urine; this tradition has been reported several times from northern Siberia. Ibotenic acid and muscimol are the active components contained by this mushroom conferring its psychotropic effects. The biochemistry and toxicology associated with the consumption of *A. muscaria* have been extensively reviewed elsewhere (e.g. Michelot and Melendez-Howell 2003). Since ancient times, the entheogenic species of *Psilocybe* have been widely used among native cultures from Mesoamerica. Before the arrival of the Spaniards in the sixteenth century, its use was recorded in various codices and colonial writings (Hernández-Santiago et al. 2017). However, there were no scientific records related to their usage, identity, and biochemistry until the middle of the twentieth century. In 1955, Robert Gordon Wasson and Valentina Wasson became the first Westerners to consume these sacred mushrooms in a ritual ceremony under the guidance of the Mazatec shaman Maria Sabina (Heim and Wasson 1958; Wasson and Wasson 1957; Wasson et al. 1974). They published their discovery in a historic article in the *American Journal Life* in 1957 (Wasson 1957). Later on, the French mycologist Roger Heim was the first to identify the species used in the rituals as *Psilocybe,* including *P. mexicana*, *P. caerulescens*, and *P. zapotecorum*, and the Swiss chemist Albert Hofmann subsequently isolated an indol that was named psilocybin (Hofmann et al. 1958). Currently, these mushrooms are still used in sacred ceremonies by Chatin, Matlatzinc, Mazatec, Nahuatl, Totonac, and Zapotec people in southwestern Mexico (Guzmán 2008).

Mushrooms consumption has been confirmed also during the European Chalcolithic. Ötzi the Iceman, who lived 5300 years ago and was discovered in 1991 at the border of Italy and Austria, carried two types of mushrooms. The first one has been identified as *Fomitopsis betulina* which has strong medicinal properties including anti-bacterial, anti-parasitic, anti-viral, anti-inflammatory, anticancer, neuroprotective, and immuno-modulating activities (Pleszczyńska et al. 2017). The second mushroom was identified as *Fomes fomentarius* which is a very well-known polypore used as a primary tinder for making fire, during millennia because basidiomata bearing traces of human handling have often been found in archaeological sites as ancient as 11,555 year old (Peintner and Pöder 2000). More than 2000 years ago in the book XVI, Chap. 77 entitled *Methods of obtaining fire from wood*, of his *Naturalia History* Pliny mentioned 'Territur ergo lignum liqno, ignem quc concipit attritu, excipiente materia aridi fomitis, fungi, vel foliorum' that can be translated as 'one piece of wood is rubbed against another, and the friction sets them on fire, which is augmented by dry tinder (aridi fomitis), especially by that of fungi and leaves' (Bostock and Riley 1855). Buller (1914) considered that the main tinder referred to by Pliny is the *amadou*, which is made from fruiting bodies of *Fomes fomentarius*. Additionally, there is evidence that this fungus has been used as medicine, due to its haemostatic and anaesthetic properties (Saar 1991a) and antitumour effects on human lung carcinoma cells (Kim et al. 2015). Anecdotally, Saar (1991a) described the ceremonial use of this mushroom among Khanty people from West Siberia, who burnt the basidiomata to produce smoke, when a person passed away until the corpse had been taken out of the house. Both uses, setting fire and healing, were fundamental in the human survival during Palaeolithic times. A clear notion of the association between oaks and edible wild mushrooms appears as early as two millennia ago in the book XVI, at the end of Chap. 11, of Pliny in his classic *Naturalia History*. He quoted 'Such is the multiplicity of the products borne by the robur 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; these last are found about its roots. Those of the quercus are the most highly esteemed'. In his interpretation of the English translation, Bostock and Riley (1855) added a footnote associated with the word mushroom by Pliny ' these were the boletus and the suillus, the last of which seem to have been recently introduced at table in the time of Pliny'. Historically, these records show the paramount importance of such fine observations made by Pliny, more than 2000 years ago, when his original publication was published between 77 and 79 A.D. Much more recently, groups of hunter-gatherers have traditionally used mushrooms as food, medicine, and flavourings in other parts of the world, using simple techniques such as dehydration by sun, wind, or heating over a fire, in order to prolong their shelf-life. We refer here to some native North American cultures (Kuhnlein and Turner 1991), who use species of *Agaricus*, *Calvatia*, *Cantharellus*, *Inonotus Lycoperdon*, *Polyporus*, and *Trichoderma* and to other ethnic groups from different parts of the world that are analysed in this book.

1.3 The Global Interwoven Web Between Mushrooms and Humans

The relationships between fungi, humans, and nature at a global level constitute a complex mosaic due to the enormous diversity of environmental, economic, social, and cultural conditions existing in the world. These have been studied with different degrees of depth in the five continents. However, it is important to recognize that there are areas where scientific knowledge of these relationships is practically nil, others in which they have received little attention and, even in those regions where more studies have been conducted, these are far from being complete. These relationships are also extremely dynamic, especially nowadays under the dramatic environmental, technological, socio-cultural, and global changes that we live. In this introductory chapter, we present some contrasting examples from various areas of the world, where scientific studies with a broad-scope have been developed, studying different aspects of wild edible mushrooms, with emphasis on ectomycorrhizal species. It is not our goal to present a complete picture of these relationships, which would be impossible, but rather to highlight and summarize the situations in various regions distributed across the five continents.

In the American continent, the relationships among mushrooms, humans, and nature can be divided into three different scenarios, those in: (1) Canada and the United States; (2) Mesoamerica, including mainly Mexico and Guatemala; and (3) South America. There are contrasting socioeconomical, historical, cultural, and biological conditions in these areas. In the case of Canada and the United States, there has traditionally been a strong scientific knowledge of the mycological diversity, only comparable with that existing in European countries. Numerous studies on the ecology, taxonomy, and use of wild edible mushrooms have historically been produced (including, for example, Molina et al. 1993; Pilz et al. 2003, 2007; Kuo et al. 2012). The commercialization of wild edible mushrooms fresh or processed, dried, powdered, or preserved in different ways, is common, and numerous companies are devoted to the marketing of this non-timber forest resource (Fig. 1.1). In contrast to the enormous mycological diversity, in general, the plant diversity in these areas is relatively small, with most of the trees being ectomycorrhizal. Cultural diversity and the associated traditional knowledge from the native human cultures have basically disappeared, and there are only few remnants of such ancient traditional knowledge. By the opposite in Mesoamerica, there is a great cultural diversity. For example, Mexico has 68 ethnic groups, each with its own culture, language,

Fig. 1.1 Diversity and commercialization of edible mushrooms in the United States of America. (**a**) Store in San Francisco selling fresh, dried, or processed edible mushrooms including ectomycorrhizal species such as chanterelle, violette chanterelle, porcini, and truffles; (**b**) Sale of porcini (*Boletus edulis* s.l.) and other edible mushrooms in San Francisco; (**c**) Wild American matsutake, *Tricholoma magnivelare*, known from eastern United States of America; (**d**) Packed wild chanterelles ready to be sold in San Francisco

world-wide vision, and natural resources management. Additionally, the biological diversity is huge (Pérez-Moreno et al. 2010), for example the country holds some of the largest diversities of ectomycorrhizal plant genera including 72 taxa of pines and 168 species of oaks. As a consequence of these cultural and biological diversities, Mexico holds one of the largest pools of wild edible mushrooms. It has been estimated that more than 450 species are currently consumed in the country (Fig. 1.2). However, this might be an underestimation due to the relatively reduced number of taxonomists who are currently active in the country. Therefore, the number of wild edible mushrooms is expected to be much larger. This huge traditional knowledge faces enormous challenges including high deforestation rates, rapid cultural erosion, emigration of young people to cities, and acculturation processes. In contrast with these realities, particularly in the last decade, there has been an awakening of the revalorization of the mycological resource. In order to preserve the forests, dozens of mushrooms fairs are carried out every year across the country organized by local ethnic groups. Mycotouristic activities have also started in different ethnic groups mainly in Central and Southern Mexico, and there have been numerous ethnomycological studies in groups which were historically obliterated in the past, for example, the Mixtec (Hernández-Santiago et al. 2016, 2017), Chinantec (López-García et al. 2017), and Tzotzil (Ruan-Soto 2018) people. Some of the Mexican groups are highly mycophilic, for example the Tlahuica people, to whom the first author of this chapter and his research team have been studying during the last 7 years, they are constituted by less than 500 persons who are able to recognize and consume more than 160 wild edible mushrooms (Fig. 1.2a). Some species such as chanterelles (Fig. 1.2b), matsutake, Caesar's mushrooms (Fig. 1.2d), morels, and porcini are exported to the United States, Canada, or Europe from Mexico. The country is one of the most important genetic reservoirs of wild edible mushrooms in the world (Fig. 1.2c).

The Central American region is one of the most diverse on the planet, particularly in terms of plants and mushrooms. Many species are related to those from the Northern and Southern hemisphere parts of the continent because this region constitutes an isthmus which connects both regions. Macrofungal diversity from Guatemala (Fig. 1.3a–c) and Costa Rica are one of the most studied in the area, where over 500 species have been recorded (Flores et al. 2012; Mueller et al. 2006).

However, the diversity is much higher, as many areas have remained unexplored, and recent molecular studies have confirmed high local endemism. For example, Del Olmo-Ruiz et al. (2017) found that fungal species richness was very high in Neotropical montane cloud forests in Mesoamerica and concluded that fungi from this region and from the Caribbean and South America are taxonomically different, with a little overlap of species recorded in these regions. It is foreseeable that Honduras, Belize, El Salvador, Nicaragua, and Panama will provide new mushroom species in the future, because large areas in these countries have remained unexplored. It is also necessary to promote studies in these regions with the support of more mycologists and with internationally funded projects that could provide knowledge and technology not available from local governments and universities. Wild edible mushrooms, especially the ectomycorrhizal ones, constitute an

Fig. 1.2 Mexican mycophily. (**a**) Tlahuica people, who are able to distinguish and consume more than 160 wild edible mushrooms; (**b**) *Cantharellus cibarius* s.l.; (**c**) Diversity of edible and sacred wild mushrooms; (**d**) *Amanita jacksonii*, one of the most preferred mushrooms among the 450 edible species known in the country

Fig. 1.3 Wild edible mushrooms from Central and South America. (**a**) Commercialization of edible mycorrhizal mushrooms (*Lactarius*, *Cortinarius*, *Ramaria*, and *Hydnum*) at San Martín Jilotepeque

important element in the diet of many rural populations in Central America. Mayan populations from Chiapas, in southern Mexico, and Guatemala are well known for their ancestral consumption of ectomycorrhizal mushrooms. In Chap. 4, a review of edible mushrooms, their habitats, and interesting ethnomycological aspects in Guatemala is presented. The country, despite its small size compared with bigger countries such as Mexico, surprises with the consumption of around 100 mushroom species by the local ethnic groups. In Honduras, the Lenca, Chortí, and mestizo indigenous populations, particularly those from the occidental zone, make use of at least 22 different species of mushroom including *Amanita jacksonii*, *A. rubescens* s.l., *Boletus pinophilus* s.l., *Cantharellus cibarius* s.l., *Lactarius indigo*, and other species in *L.* sect. *Deliciosi*, and, *Hydnum repandum*; all of these coming from pine-oak forests and locally known as *choros*, *juanillas*, *chequecas*, or *canturinas* (Vega 2018; Sarmiento and Fontecha 2015; Marineros et al. 2015). In El Salvador, despite its scarce native forests, the most known and demanded mushroom is the *tenquique* (*Pseudofistulina radicata*), but the local consumption of species belonging to *Cantharellus*, *Amanita,* and *Lactarius* is also important. The highest fungal diversity of the country can be found in the montane cloud forests from the volcanic chain, where more than 100 wild species have been identified (Aguilera 2016), including new species of *Laccaria* and *Boletales* (Delgado 2010; Toledo 2013). Nicaragua has been scarcely studied but the country should hold unique wild species in pine-oak forests, the stands of *Pinus caribaea* and its extensive savannahs (Stevens et al. 2001). Despite the fact that mainly saprotrophic species have been recorded to date, the potential existence of edible ectomycorrhizal species is almost certain. Costa Rica and Panama are one of the most important megadiverse countries of the planet. There have been at least four books that show the richness of the fungal diversity from Costa Rica, including a surprising number of species associated with local oaks that resemble those from the Northeastern region of the continent (Halling and Mueller 2002). Nevertheless, and despite the high diversity consumption of wild edible mushrooms is low, which might be explained by the small indigenous population compared to those existing in the rest of the region. Panamá, which possesses one of the most important neotropical forests of the continent, also has some well-known edible mycorrhizal species such as *Lactarius indigo* and *Laccaria* spp.; however, local consumption of mushrooms is also low and in general the country has been considered as mycophobic (Vega and de León 2018). Central America is quite a singular territory on the planet that deserves to be studied at a deeper level. The influence of its tectonic-volcanic origin, its location among the oceans, the rich native biodiversity, as well as the different ancestral cultures, including the Maya culture, make this region an almost unopened treasure

Fig. 1.3 (continued) market in Guatemala; (**b**) Mari Flor Gómez Chalí, student of Universidad de San Carlos with fresh *Lactarius* at San Juan Sacatepéquez market in Guatemala; (**c**) Gabriel González collecting the edible saprotrophic mushroom *Pseudofistulina radicata* near Antigua, Guatemala; (**d**) *Suillus luteus* known as *callampas* growing in plantations of *Pinus radiata* Biobío, Chile; (**e**) Trade of *Cyttaria* sp., known as *digüeñe* o *dihueñe* which grows in *Nothofagus* forests in Biobío, Chile; (**f**) *Rhizopogon* sp. known as *papitas* (little potatoes), an ectomycorrhizal mushroom in exotic plantations of *Pinus radiata* in Los Ángeles, Chile that offers knowledge and answers to current discussion regarding conservation and sustainable use of natural resources. Local wild edible mushrooms are not only the result of their inherent capability to adapt and evolve but they can also be a source of food and income. They are an example of appreciation and respect from humans towards nature and an important source of secondary metabolites useful in the green and medicinal industries. The situation in Central America can be summarized in the statement pointed out by Piepenbring et al. (2011) for the mushrooms of tropical Panama 'highly diverse, mostly unknown, and further mycological field work is urgently needed because habitats are being destroyed and fungi specific to them are lost forever'. Meantime, the checklist of fungi in Panama contains more than 2700 species (Piepenbring 2013).

In South America, despite the enormous diversity and the presence of ethnic groups, the diversity of wild edible mushrooms remains poorly explored in most of the countries due to the complex political and social situations. However, some studies are being developed in some south-American countries. For example, in Chile, the consumption of *Suillus* species, called 'callampa' constitutes an important income for the owner of pine plantations, due to their high productivity. These edible ectomycorrhizal mushrooms can be frequently found in domestic stores packed by a number of companies usually dried and sliced (Fig. 1.3d). Also, other ectomycorrhizal mushrooms from *Rhizopogon*, known as *papitas* (little potatoes) are consumed in young stages (Fig. 1.3f). One of the most characteristic species is *Cyttaria* spp. coming from *Nothofagus* forests, which is sold in domestic markets (Fig. 1.3e). Two chapters in this book deal with the mushroom diversity in Colombia and Argentina.

The situation in Europe is highly diverse. There are mycophilic and mycophobic countries; the mycobiotas of a number of countries have historically been studied while others (mainly in eastern Europe) have received less attention; the strongest and oldest evidences of mushrooms used by humans have been recorded in this continent; and the commercialization of a wide variety of edible, medicinal, and nutraceutical mushrooms ranges from fresh to entirely processed products (Fig. 1.4). As several chapters of this book (Chaps. 7–9, 12, and 13) deal with detailed analyses of the situation in this continent, they will not be discussed further here.

Africa is the world's second-largest continent with more than 30 million km^2 covering approximately 20% of the Earth's land. From the mycological point of view, it continues being a mysterious continent full of surprises and largely unexplored. Northern Africa, including the Atlas Mountains with abundant *Cedrus atlantica*, *Quercus*, and *Pinus* forests is extremely rich in wild edible mushrooms including black truffles, chanterelles, morels, black trumpets, and species of *Ramaria*. In arid and subarid regions, proliferates one of the most attractive complexes of fungal species: the desert truffles, included mainly in the genera *Terfezia* and *Tirmania*. These truffles establish ectomycorrhizal associations with shrubs in the family Cistaceae and also with oak and pine trees. They constitute an important source of food for marginal groups including Berbers or Amazighs in Morocco, Algeria, Tunisia, and Libya. The technique used, mainly by women, to gather these truffles is heart-breaking: the women hit the soil with a stick, until they detect, based

Fig. 1.4 Aspects of useful wild mushrooms in Europe. (**a**) Truffle hunting in a Southern Spain forest; (**b**) *Fomitopsis betulina* growing on birch in Bolzano, Northern Italy (this is the mushroom that Otzi the iceman was carrying 5300 years ago); (**c**) *Laetiporus sulphureus*, the chicken of the woods, a highly esteemed edible wild mushroom around the world, growing on beech in a North Yorkshire forest in central England; (**d**) Fresh Porcini mushrooms (*Boletus* spp.) known as 'the king of the mushrooms' in Southern Ukraine; (**e**) Commercialization of processed products mostly including black truffles, porcini, and morels in Cahors, France

on their enormous experience, a different sound emitted by the different texture of the soil where the ascomata of the desert truffles grow. Then, they remove the surface soil to collect the ascomata. Gathering 1 kg of truffles implies to be crouched down for hours daily (Fig. 1.5a) in order to get food or currency to survive (Fig. 1.5b). In the scenario of sub-Saharan Africa, there are some similitudes and differences compared with that of northern Africa. Infinitely rich in ecotypes, biodiversity, natural resources, and traditions, the sub-Saharan Africa is also a treasure box full of

Fig. 1.5 People and edible mushrooms in Africa. (**a**) Berber woman collecting desert truffles, hitting the soil with a stick in a traditional way in Morocco; (**b**) Tajine of dessert truffles *Terfezia* spp. in Morocco; (**c**) Dr. N'golo Kole taking a bite of *Termitomyces shimperi* in Togo; (**d**) One of the rare occasions where local people were collecting boletes in Malawi; (**e**) Children assist in the selling of *Cantharellus platyphyllus*, *C. congolensis*, and *C. rufopunctatus* in Malawi; (**f**) *Cantharellus* harvest of the day in Burundi; (**g**) Mixture of *Lactifluus*, *Cantharellus*, and *Amanita* at a colourful market in Tanzania

edible mushrooms (Fig. 1.5c–g). There, the ethnomycological pathways are as diverse as the vegetation types and ethnical groups. Some populations do not eat wild mushrooms at all, but in many areas, fungi constitute a very important part of the local diet. Especially in countries were ectomycorrhizal trees dominate the vegetation, the traditional knowledge and use of edible mycorrhizal mushrooms is historical and highly significant. Although also present in the tropical rainforest (where they occur among other fungi with local clusters of *Gilbertiodendron* trees), ectomycorrhizal fungi are most abundant and form the largest fruiting bodies in subtropical woodlands: the Sudanian woodlands in West Africa, the Zambezian woodlands (miombo woodlands) in East, Central, and Southern Africa. Miombo woodlands form the most extensive vegetation type (across 2.8 million km^2) in Africa and are seasonally dry deciduous woodlands (White 1983; Frost 1996). These woodlands are dominated by trees of the leguminous genera *Brachystegia*. The name miombo refers to species of the genus *Brachystegia* (Smith and Allen 2004), *Julbernardia*, and *Isoberlinia* (Caesalpinioideae). The most popular edible fungi genera associated with these trees are *Cantharellus*, *Amanita*, *Russula*, *Lactifluus* and to a lesser extent *Lactarius*. The same genera (often represented by different species) are preferred and collected in many West African countries covered in Sudanian woodlands. Boletes are very common and represented by many genera and species but, strangely enough, usually not consumed. Apparently the changing colour by oxidation, a phenomenon common in many boletes, and the soft, spongy texture once they are mature, are characteristics that make them very unappetizing for indigenous people. All but three countries on the list of 25 poorest countries in the world are sub-Saharan African countries. Hence, it should come as no surprise that especially in rural areas of the least developed countries, people are very dependent on non-timber forest products as an important supplement to their crops. The arrival of the rain season, and of the first mushrooms with it, means the end of the dry season and the end of the traditional famine period because the food reserves are exhausted and the mushrooms pop up faster than the newly planted crops. Especially women and children are collecting for their own supplies but also to sell part of the harvest at local markets or along the road. Wild edible mushrooms play an important role in the diet of local people in East Africa and neighbouring countries (Buyck 1994; Morris 1984; Pegler and Piearce 1980; Rammeloo and Walleyn 1993; Härkönen et al. 2003). According to Degreef (1992), yearly consumption can be estimated at 30 kg/inhabitant in rural areas, and 15 kg/inhabitant in the city for the wet (and thus production) season only. Natural miombo forest produces on average of 150 kg edible mushrooms/ha every year (De Kesel et al. 2017). But this huge production is under threat. In some woodlands, the rainy season is restricted and unimodal; in other parts, a longer rainy season is separated by a short dry period from the second rainy season. The length of the dry season is variable and dry season fires commonly occur, but a changing climate also means an unreliable wet season, shifting in time in some countries, or even completely lacking. It goes without saying that this has an important effect on the availability of the edible mushrooms for the local people. Furthermore, the forests are often mismanaged and over-exploited, and turned into cropland and pastures, or replaced by exotic plantations at an alarming rate. Unsustainable utilization leads to impoverishment of the ecosystem's integrity and long-term survival/productivity, which in turn reduces revenues derived from the forest. Moreover, watersheds get degraded and together with erosion lead to desertification. In some countries (e.g. Ivory Coast), where much of the original woodland has been replaced by plantations or secondary forest, people tend to eat more saprotrophic species, especially wood-decayers and litter saprotrophs. Popular genera are *Pleurotus*, *Lentinus*, *Volvariella*, and *Chlorophyllum*. The latter genus has a dubious reputation because of the toxic *C. molybdites*, but a recent molecular study (Ge et al. 2018) showed that four more species are common in Africa, among which are the edible *C. palaeotropicum and C. hortense*. It is also with those groups of saprotrophic species that we see cultivation programs with low-cost technology originating. Even the cosmopolitan *Schizophyllum commune* is cultivated in some African countries (Osemwegie et al. 2014). A popular and delicious genus occurring as well in the woodlands as in gardens and plantations is *Termitomyces*, associated with termite hills. The taste and texture of *Termitomyces* species, from the very small *T. microcarpus* (which you have to collect by the hundreds to fill a plate) to the giant *T. titanicus*, the largest edible mushroom in the world, are excellent. When conducting ethnomycological research in Africa and asking people about their general appreciation of mushrooms as food, it is interesting to notice that they rank mushrooms somewhere between chicken and crocodile (pers. obs. in Zimbabwe) or between chicken and fish (pers. obs. in Malawi, Togo). They consider them meat rather than vegetables, which is exactly the opposite to the general opinion in many temperate countries where people still consider fungi to be plants and mushrooms a kind of vegetable. Up to 20 years ago, an important part of these species harvested and offered for sale only had local names and were new to science. But in this molecular era where the importance of world-wide sampling becomes more and more clear, the interest in African mycology is also increasing. Recently, ectomycorrhizal groups such as chanterelles (Buyck et al. 2013) and milkcaps (Verbeken and Walleyn 2010) were the subject of many studies. Good descriptions, pictures, and identification tools are more common now and stimulate mycologists inside and outside Africa to contribute to the exploration of the diversity. Moreover, some recent publications focus purely on edible mushrooms taking into account the new phylogenetic insights (De Kesel et al. 2017; Härkönen et al. 2015).

In Asia, the highest diversity of edible ectomycorrhizal mushrooms is harboured by China. Due to the diverse habitats and plant species created by the great variation in climate and topography, China has the world's richest diversity of wild edible mushrooms, with 1020 edible species recorded (Wu et al. 2019), around 75% of which are distributed in Southwestern China. Additionally, 692 medicinal species have been recorded in the country, including the world-wide famous Lingzhi (*Ganoderma spp*.) which is a mushroom that has been renowned in China for more than 2,000 years (Cao et al. 2012). Every county in Yunnan has at least one mushroom market trading wild edible mushrooms harvested from surrounding forests (Fig. 1.6a). At the main markets such as in Kunming and Nanhua, hundreds of tons of wild edible mushrooms change hands daily during mushroom season from June

Fig. 1.6 Aspects of wild edible mushrooms in China. (**a**) Mushuihua wild edible mushroom market at Kunming; (**b**) *Thelephora ganbajun* at Ciba wild edible mushroom market, Kunming; (**c**) *Tricholoma matsutake* young fruiting bodies at Shangri-La wild edible mushroom market; (**d**) An experimental plantation for the cultivation of *Tuber indicum*; (**e**) Commercialization of *Tuber indicum* in Yunnan; (**f**) *Lactifluus volemus* sold in southeastern Yunnan

to October. A total of 321 species, belonging to 101 genera, and 47 families have been identified as wild mushrooms traded in the local markets. Of these commercial mushrooms, Boletaceae was the best represented family, with 27 genera and 23.05% (74 spp.) of the total species. *Ramaria* being the most species-rich genus in the Gomphaceae family, with 22 species and 6.83% of the total (Wang and Liu 2002; Wang et al. 2004; Yu and Liu 2005; Dai et al. 2010; Cui et al. 2015; Tang et al. 2015; Wu et al. 2015; Yang 2015). More than 164 species commonly traded and 60 dominant commercial species in the genera *Boletus*, *Cantharellus Lactarius*, *Ramaria*, *Russula*, *Termitomyces*, *Thelephora* (Fig. 1.5b), *Tricholoma*, *Tuber*, etc. are found in the Yunnan's local markets. The foreign income produced from wild mushroom exportation is over US$100 million every year in China. Marketing of *Tricholoma matsutake*, and a few additional species, such as *Ophiocordyceps sinensis*, *Tuber indicum*, and *Boletus bainiugan*, has significantly improved the local economy in the last few years (Wang and Yang 2006). Harvesting wild mushrooms is an important livelihood and generates 15–90% of these people' annual income. In the last 10 years, over 1000 tons 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 the Shangri-La region, northwest Yunnan, harvesting matsutake can result in an annual return of over 10,000 Chinese Yuan (about US$1500) for an average family. The natural production of wild edible mushrooms has declined since large-scale commercial harvesting started in the 1990s. A variety of efforts have been deployed to protect wild edible mushrooms. The most important 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 (Fig. 1.6c) and truffles. Experimental plantations have been set up for truffle cultivation, and the production of *T. indicum* has begun (Fig. 1.6d). Other attempts to cultivate truffles (*T. borchii*, *T. melanosporum,* and *T. sinoaestivum*), milk cap mushrooms (*Lactarius deliciosus*, *L. hatustake*, and *L. vividus*), and to understand the biology, ecology, and cultivation potential of edible mushrooms are being undertaken (Geng et al. 2009; Wang et al. 2019). However, conservation of the precious wild edible mushroom remains a vital and urgent issue (Fig. 1.6e–f).

Australasia constitutes a very unique continent from the biogeographic, historic, and biodiversity perspectives. New Zealand is exceptional in many aspects, and edible mushrooms of Aotearoa are no exception. From a geological point of view, New Zealand has been isolated from all other continents for 80 million years (Dawson and Lucas 2000; Wallis and Trewick 2009), and this situation has generated a high level of endemism, as well as extraordinary features such as the lack of land mammals (except bats) and flightless birds like the iconic kiwis (Murphy et al. 2019). From a human point of view, New Zealand was mass-populated only very recently, first about 700 years ago by Māori people from the Pacific (Walter et al. 2017) followed by European then worldwide settlers since about 350 years. These characteristics created a very original situation for mushrooms. Except Southern beech forests (*Nothofagus* spp.), which are confined to specific areas, most native New Zealand trees (i.e. magnificent Podocarps and other conifers such as Kauri) live symbiotically with arbuscular mycorrhizal fungi and therefore do not produce ectomycorrhizal fruiting bodies (Orlovich and Cairney 2004). Native ectomycorrhizal fungi are associated only with three woody plant genera, *Nothofagus*, *Leptospermum*, and *Kunzea*, and are very different from ectomycorrhizal fungi associated with Fagaceae and Pinaceae in the Northern Hemisphere (Orlovich and Cairney 2004). The short period of human colonization also explains the lack of knowledge concerning the edibility of mushrooms found in beech forests. Several saprotrophic fungi endemic to New Zealand are closely related to commercial

Fig. 1.7 (**a**) *Cyclocybe* (*Agrocybe*) *parasitica* fruiting on poplar, Lincoln Farm of the New Zealand Institute for Plant & Food Research (PFR), Lincoln, New Zealand; (**b**) *Boletus edulis*, Christchurch, New Zealand; (**c**) Cultivated *Lactarius deliciosus*, PFR-Lincoln Farm; (**d**) *Tuber borchii* (bianchetto truffle) plantation (to the right of the picture) on the PFR-Lincoln Farm, note the white tags corresponding to bianchetto truffles marked in the grassy aisle alongside the truffière; (**e**) the dog Mila, a vizsla and wonderful bianchetto expert, PFR-Lincoln plantation; (**f**) Cultivated bianchetto truffles, PFR-Lincoln Farm; (**g**) Tewnion Truffière, Canterbury, New Zealand; (**h**) An amazing 'truffle machine', the spoodle Cassie hidden by her harvest of Périgord black truffles at Tewnion Truffière; (**i**) A Périgord black truffle (*Tuber melanosporum*) grown at Tewnion Truffière, cut and photographed by Chef Vaughan Mabee of Amisfield, Central Otago, New Zealand; (**j**) The first Canterbury Truffle Festival, Riccarton Market, Christchurch, July 2015, has launched a series of winter truffle attractions now popular in Canterbury; (**k**) Participants of the New Zealand Truffle Association' 2019 conference in Christchurch visiting a black truffle plantation during the post-conference field trip; (**l**) Pleasure for the eyes and the mouth made with the Périgord black truffle by Chef Vaughan Mabee of Amisfield, Central Otago, New Zealand

species of the northern hemisphere, e.g. *Lentinula novae-zelandiae* a Shiitake relative (Johnston 2009), *Cyclocybe* (*Agrocybe*) *parasitica* (Fig. 1.7a) a Poplar mushroom relative (*A. cylindrica*) (Cooper 2012). Some New Zealand species are recently the object of cultivation trials (Buchanan pers. comm.) and would greatly complement the currently limited choice of cultivated exotic mushrooms (mostly *Agaricus bisporus* followed by *Pleurotus pulmonarius* and *Lentinula edodes*). A few wild edible saprotrophic species present in New Zealand are exotic, e.g. *Agaricus campestris*, *A. arvensis*, *Marasmius oreades*, *Lepista nuda*. Regarding ectomycorrhizal mushrooms, the arrival of Europeans has considerably changed the situation: early settlers brought with them broadleaf trees and conifers from Europe and, in doing so, imported accidentally several edible ectomycorrhizal mushrooms associated with these trees: Porcini (*Boletus edulis* s.l.) (Wang et al. 1995) (Fig. 1.7b), Slippery jack (*Suillus luteus*), Shoro (*Rhizopogon rubescens*), Birch bolete (*Leccinum scabrum*) while other famous edible species never made it to New Zealand by accident, e.g. economically valuable Truffles (*Tuber* spp.) (Bulman et al. 2010), Chanterelles (*Cantharellus cibarius* s.l.), Milkcaps (*Lactarius* section *Deliciosi*) (Fig. 1.7c), Caesar's mushroom (*Amanita section Caesarea*), etc. Interestingly, nowadays, New Zealand has developed an important agricultural economy based on the cultivation, or farming, of exotic plant and animal species: kiwifruit (native to China), grapevine, cattle and dairy farms, sheep, pine timber, etc. Again, edible mycorrhizal mushrooms are no exception. In the late 1970s, Dr. Ian Hall, an arbuscular mycorrhiza scientist inspired by European researchers working on truffle cultivation, envisioned to grow these delicacies in New Zealand. Free of the cultural bonds that characterized many European truffle experts and growers, he dared raising the pH of agricultural farm land up to levels compatible with the cultivation of the Périgord black truffle (*Tuber melanosporum*) (pH $\approx$ 8), by adding considerable amount of lime. The efforts of his team were rewarded in 1993 when a truffle orchard in Gisborne produced the first ascocarp of *T. melanosporum* ever produced in the southern hemisphere (Guerin-Laguette 2008). This triggered the development of a truffle and edible mycorrhizal fungi industry in New Zealand. After years of patient incubation and technical challenges, New Zealand is now producing over a ton of truffles in commercial truffières, mostly *T. melanosporum* and *T. borchii* (Fig. 1.7d–i), and also *T. aestivum*, *T. brumale*, as well as commercial quantities (in very restricted areas to date) of saffron milk caps (*Lactarius deliciosus*) in pine orchards (Wang et al. 2019; this book, Chap. 5). Like truffles, saffron milk cap were successfully introduced purposely to New Zealand as part of a research programme initiated in 1997. New Zealand has now the opportunity, through further applied and basic research, to grow a profitable and sustainable edible mycorrhizal fungi industry that can fit with its lifestyle and image of gourmet country, further attracting tourists from all over the world (Fig. 1.7j). For almost 30 years, The New Zealand Truffle Association (NZTA) has pioneered and supported the development of an edible mycorrhizal fungi industry in New Zealand. The NZTA organizes a national conference every year (Fig. 1.7k). The Périgord black truffle, black diamond of the French cuisine, is now inspiring very talented New Zealand chefs (Fig. 1.7l). More high value ectomycorrhizal fungi could be cultivated in the future, either native or exotic, providing that biotechnical and biochemical research is carried out to demonstrate their value and to show that the proposed cultivation of selected, new, exotic species (e.g. pine-specific *Lactarius sanguifluus*) in already disturbed environments would increase overall biodiversity without having negative impact on native areas of New Zealand.

Acknowledgements The credit pictures are as follows: Figs. 1.1a–d and 1.3a–c are from Roberto Flores Arzú; Fig. 1.5c–g are from Annemieke Verbeken; Fig. 1.4d is from Alexander Bondarchuk; Fig. 1.6a–d are from Fu-Qiang Yu; Fig. 1.2c is from Lucila Aragón Carrillo; Fig. 1.2d is from Jorge Manuel Mejia Bojorquez; Fig. 1.3c is from José María González; Fig. 1.3d–f are from José Leonardo García Rodríguez; Fig. 1.7, all photos are by The New Zealand Institute for Plant & Food Research except Fig. 1.7b, courtesy Wang Yun; Fig. 1.7e, courtesy Will Clayton; Fig. 1.7g, h, courtesy Wayne Tewnion; Fig. 1.7i, l, courtesy Vaughan Mabee; Figs. 1.2a, b, 1.4a–c, e, 1.5a, b and 1.6e, f are from Jesús Pérez-Moreno. Alexis Guerin-Laguette is grateful to Nicholas Cummings for helpful suggestions on the Australasia section. Jesús Pérez-Moreno acknowledges the financial support from CONACyT 2018-07-01EXTV and COMECyT EST2018-005 to develop a sabbatical stay at the Kunming Institute of Botany, Kunming, China.

Funding from the CONACyT project “Biotechnologies of highly-prized or bioculturally-important edible ectomycorrhizal mushrooms for reforestation with native Mexican trees using frontier scientific methodologies” is also acknowledged.

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