

# Chapter 2

## Systematics and Ecology of Edible Ectomycorrhizal Mushrooms

Matthew E. Smith and Gregory M. Bonito

### 2.1 Introduction

#### 2.1.1 *Humans and Edible Fungi*

Humans have consumed fungi for sustenance, medicine, and culinary delight since ancient times. Some fungi are purposely cultivated, but most edible fungi are gathered from the wild. The Romans and Greeks treated mushrooms as a special kind of food (Miles and Chang 2004), and there is historical evidence of mushroom consumption in ancient India (Chopra 1933) and Mesoamerica (Ruan-Soto et al. 2006). There are also reports of the use of fungi by the indigenous cultures of South America (Henkel et al. 2004), Africa (van Dijk et al. 2003), Australia (Trappe et al. 2008), and Asia (Yun et al. 1997). The rapid emergence of mushrooms and other fungal fruiting structures has long been shrouded in mysticism, as suggested by common names for fungi such as “toadstool,” “Elvin saddle,” “witches’ butter,” and “fairy ring.”

There are deeply held superstitions and misunderstandings regarding mushrooms and truffles. For example, the Romans believed that truffles were the result of lightning strikes or thunderclaps; truffles were collected both because of their strong flavors but also because of their status as “mysterious products of the earth” (Hall et al. 2007). Similarly, mushrooms that fruit in circular patches or “fairy rings” were said to be the paths left by fairies that danced in the night (Morgan 1995). Nonetheless, through keen observation of fungi in their natural habitats, humans have observed that some fungi depend directly on the dung, wood, insects, or grains where they are found. However, the fruiting of mushrooms and truffles

---

M.E. Smith (✉)

Department of Plant Pathology, University of Florida, Gainesville, FL 32611, USA

e-mail: [trufflesmith@ufl.edu](mailto:trufflesmith@ufl.edu)

G.M. Bonito

Biology Department, Duke University, Durham, NC 27708, USA

e-mail: [gmb2@duke.edu](mailto:gmb2@duke.edu)

directly on soil and not associated with particular substrates has long remained a perplexing mystery. Part of the problem is that most fungi spend the majority of their life cycle growing in opaque substrates such as soil or wood, and this makes them particularly challenging to study. For many fungi, their sporocarps are the only visual cue to alert humans to their presence. However, fungal hyphal networks abound underfoot whenever we walk through forests and other natural habitats.

### ***2.1.2 Discovering the Ectomycorrhizal Symbiosis***

A major breakthrough in understanding the biology of soil- and root-dwelling fungi came in 1885 when German biologist A.B. Frank published an important paper on the association between truffles and trees (Frank 2005). He suggested that many soil-dwelling, plant-associated fungi were actually living in a mutualistic symbiosis with trees. He coined the term “mycorrhiza” (from the Greek linguistic roots “myko” meaning fungus and “rhiz” meaning root) to explain this close relationship. Although the debate about the validity and significance of mycorrhizas continued over the ensuing decades, we now understand the key ecological roles that mycorrhizas play in most ecosystems on earth (Smith and Read 2008). Biologists currently recognize at least four distinct types of mycorrhizal associations (e.g., ectomycorrhizas [EM], arbuscular mycorrhizas, ericoid mycorrhizas, and orchid mycorrhizas), but only EM fungi routinely produce large, fleshy fruiting bodies that are consumed by humans. Recent estimates suggest that at least 6,000 plant species and 20,000 fungal species are involved in this ecologically and economically important symbiosis (Rinaldi et al. 2008; Brundrett 2009).

A.B. Frank’s original research focused on EM associations of truffles (*Tuber*, *Ascomycota*), but subsequent work has shown that many different groups of fungi form ectomycorrhizas, including species of *Ascomycota*, *Basidiomycota*, and at least one order in the *Zygomycota* (*Endogonales*, *Mucoromycotina*) (Tedersoo et al. 2010). Because EM fungi are often difficult to isolate in pure culture (Melin 1954) and challenging to work with under laboratory conditions (Palmer 1969), much of the early EM research was observational in nature or necessarily focused on a few fungi that could be readily manipulated [e.g., *Pisolithus arhizus* (Scop.) Rauschert (= *Pisolithus tinctorius*), *Rhizopogon* spp.] (Melin and Krupa 1971; Marx 1977). Studies from fumigated nursery soils demonstrated early on that at least some plants depend on EM fungi for normal growth and reproduction (e.g., *Pseudotsuga menziesii* (Mirb.) Franco) (Trappe and Strand 1969). EM fungi have subsequently been found to be integral for plant nutrition (particularly the acquisition of N and P) as well as in the mitigation of drought stress and root pathogens (Marx 1970; Parke et al. 1983; Smith and Read 2008).

### 2.1.3 *Edible Plant-Associated Fungi that Do Not Form Ectomycorrhizas*

Although EM fungi fruit from soil in association with plant roots, the simple occurrence of a fungal fruiting body with tree roots does not prove that the fungus is an EM symbiont of plants. There are several well-known cases where edible mushrooms consistently fruit near particular plants but are not EM symbionts. One example is the distinctive “Ash Bolete,” *Boletinus merulioides* (Schwein.) Murrill, which only fruits near trees in the genus *Fraxinus* (Ash). Despite belonging to the Boletineae (Boletales, Basidiomycota), a phylogenetic group with many EM species, this fungus does not form ectomycorrhizas but instead forms a commensalism with insects that feed on *Fraxinus* roots (Brundrett and Kendrick 1987). Morels (*Morchella* spp., Morchellaceae, Pezizales, Ascomycota) are another example. Morels are often found in association with plants that do not form ectomycorrhizas (e.g., *Malus* [apple], *Ulmus* [elm], and *Liriodendron* [tulip poplar]) or in coniferous forests that have been recently burned (Winder 2006). Although morels have been shown to associate biotrophically with roots under some conditions (Dahlstrom et al. 2000), they are not found in EM community studies, they can survive as sclerotia, and they do not need a host plant to complete their life cycle (Ower 1982; Miller et al. 1994).

## 2.2 Ectomycorrhizal Fungi and the Molecular Revolution

Since the time of A.B. Frank, the challenges in determining the ecology and trophic mode of fungi based on observational data were a significant obstacle. However, PCR-based molecular approaches for studying EM fungi have clarified our understanding of these important microbial plant symbionts (Horton and Bruns 2001). Since pioneering molecular studies of EM fungi in the 1990s (Bruns et al. 1989; Gardes and Bruns 1996), DNA-based tools have figuratively “peeled back the soil” to reveal important insights about three key aspects of EM fungi: (1) community ecology, (2) population biology, and (3) molecular systematics.

### 2.2.1 *Community Ecology*

The first molecular tools that helped elucidate the biology of EM fungi were basic “DNA fingerprinting” techniques such as RFLP (restriction fragment length polymorphism). These techniques are relatively inexpensive and can be used to identify EM fungi from sporocarps or directly on EM roots (Gardes and Bruns 1996). For species-level identification, basic DNA fingerprinting approaches have now been largely supplanted by DNA sequence-based methods that typically offer

higher accuracy and resolution (e.g., DNA barcoding). DNA barcoding refers to the sequencing of a particular locus that is considered to be species specific and can thus be used to identify fungi at the species level based on the DNA sequence. The internal transcribed spacer region (ITS) of the ribosomal DNA (rDNA) has long been the marker of choice for ecological studies of fungi, and this DNA region has recently been recognized as the “official barcode” for the kingdom (Seifert 2009; Schoch et al. 2012). ITS rDNA barcodes provide direct identification of morphological EM types (e.g., “morphotypes”) when they can be directly matched to reference sequences from well-identified specimens. When direct matches are not made, ITS rDNA sequences provide at least some phylogenetic signal to help identify the fungal lineage to which the EM species belongs. In cases where ITS sequences are not sufficient for delimiting species, other informative loci may be targeted [e.g., ribosomal large subunit (LSU or 28S), elongation factor (EF1 $\alpha$ ), second subunit of RNA polymerase (RPB2)].

Molecular fungal community studies based primarily on ITS rDNA have provided several important insights about the biology of EM fungi: (1) the diversity of EM fungi is higher than expected (both at species and lineage levels); (2) species common as sporocarps are not always abundant on roots; (3) species that are frequently found on roots are not always encountered as sporocarps; (4) many abundant fungi as EM on root tips make inconspicuous sporocarps that are resupinate or sequestrate (truffle-like); (5) it is common to encounter cryptic species within fungal community studies such that two or more distinct, divergent species exist within one morphological species; (6) biogeographic patterns of EM fungi are more similar to those of plants and animals than those of *Bacteria* and *Archaea*; (7) local EM community structure is strongly influenced by dispersal, host plant species, and resource availability; and (8) different phylogenetic groups respond differently to resource fluctuations, disturbance, and management (Horton 2002; Lilleskov et al. 2002; Peay et al. 2007; Smith et al. 2007a, b; Diaz et al. 2009) (see also Chap. 7).

### 2.2.2 *Population Genetics*

One big mystery for biologists interested in the ecology of EM fungi has been to discern “what is an individual EM fungus and what does it do?” For example, does an individual EM fungus produce many sporocarps or just a few? Do they encompass large areas of forest or do they exist in small patches? Do they fruit each year or is fruiting reserved for optimal conditions? Throughout the last several decades, while molecular studies were elucidating the community structure of belowground EM fungi, population genetic studies were clarifying the size of fungal genets (i.e., fungal individuals) and dispersal patterns of many key EM fungi. A recent paper on population genetics of EM fungi exhaustively reviews the subject (Douhan et al. 2011), so we will address the topic only briefly here.

Population genetics studies of EM fungi first used culture-based somatic incompatibility tests to examine genet size and distribution on the landscape. However,

because this approach depends on living axenic cultures, culture-based studies were limited to only those fungal species with significant saprotrophic abilities. Furthermore, variable molecular markers such as RAPDs (randomly amplified polymorphic DNA) have been shown to be superior to culture-based approaches for delimiting fungal genets (Jacobson et al. 1993). More recent studies have utilized microsatellites, which have the advantage that they are specific, nondominant markers that can be used to study EM fungi directly on roots, as sporocarps or as pure culture isolates (Kretzer et al. 2005).

Although most EM fungi population studies have focused on a few EM lineages (e.g., *Hebeloma*, *Boletus*, *Laccaria*, *Tricholoma*, *Russula-lactarius*—see below), they have revealed great variations in population structure and in life-history strategy between members of different lineages. For example, species of *Amanita*, *Laccaria*, *Hebeloma*, and Russulaceae tend to have small genets (usually less than 5 m across), whereas species of *Boletus*, *Suillus*, and other Boletales tend to have large genets (often 10–20 m across but sometimes up to 100 m in diameter). Similarly, members of the EM lineages differ in their ability to persist in the environment. Some groups appear to survive only 1–3 years and are continually establishing new individuals from spores (e.g., Russulaceae, *Laccaria*), whereas other groups have genets that are perennial and may persist up to 35 years in some cases (e.g., many Agaricales and Boletales) (Baar et al. 1994). These patterns are interesting, especially when considered along with other phylogenetically linked traits (e.g., EM exploration strategies—Table 2.1).

Population genetic studies have definitely provided important insights into the diversity of life-history strategies among EM fungi, but there are still many aspects that have not been adequately addressed. In particular, unexplained variation within lineages and even genera suggests that additional studies are needed. In addition to the problem of variation within and among groups, more than two-thirds of the population studies on EM fungi have been conducted in the USA or Europe, and only a few tropical EM fungi have been studied from a population biology perspective (Douhan et al. 2011). Furthermore, many fungal lineages and genera that produce economically important sporocarps have yet to be studied (e.g., *Terfezia* and *Tirmania* spp. in the *terfezia-peziza depressa* lineage, *Craterellus* and *Hydnum* spp. in the *cantharellus* lineage).

### 2.2.3 Molecular Systematics

While molecular markers were being used to explore the community ecology and population biology of EM fungi, similar molecular tools were being paired with phylogenetic methods and advances in computing power to map the evolutionary tree of life (Bruns et al. 1989). Although PCR and DNA sequencing have fundamentally changed our understanding of the entire evolutionary tree of life over the last 20 years, no branch of the tree has been reorganized more thoroughly than the kingdom Fungi (James et al. 2006). Once thought to have evolved only a handful of

**Table 2.1** Genera and lineages of ectomycorrhizal fungi with edible fruiting bodies

Genus	EM lineage	Order (Phylum)	Edibility	Ectomycorrhizal exploration type	References
<i>Afroboletus</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Boa (2004)
<i>Albatrellus</i>	/albatrellus	Russulales (Basidiomycota)	E	Ms	Arnolds (1995)
<i>Alpova</i> <sup>3</sup>	/paxillus-gyrodon	Boletales (Basidiomycota)	E	L <sup>5</sup>	Trappe et al. (2007)
<i>Ananita</i> <sup>1,3,4</sup>	/amanita	Agaricales (Basidiomycota)	\$	Ms	Arnolds (1995)
<i>Arcangeliiella</i> <sup>3</sup>	/russula-lactarius	Russulales (Basidiomycota)	E	C, S, Ms <sup>5</sup>	Trappe et al. (2007)
<i>Aureoboletus</i>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Arora (1986)
<i>Austroboletus</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Balsamia</i> <sup>3</sup>	/tuber-helvella	Pezizales (Ascomycota)	E	C	Trappe et al. (2007)
<i>Bankera</i>	/tomentellopsis-bankera	Thelephorales (Basidiomycota)	E	L	Boa (2004)
<i>Barssia</i> <sup>3</sup>	/tuber-helvella	Pezizales (Ascomycota)	E	C <sup>5</sup>	Trappe et al. (2007)
<i>Boletellus</i>	/boletus	Boletales (Basidiomycota)	E	L	Bessette et al. (1997)
<i>Boletopsis</i>	/incertae sedis	Thelephorales (Basidiomycota)	E	Mm	Arora (1986)
<i>Boletus</i>	/boletus	Boletales (Basidiomycota)	\$	L	Arora (2008)
<i>Cantharellus</i>	/cantharellus	Cantharellales (Basidiomycota)	\$	Ms	Arnolds (1995)
<i>Catathelasma</i> <sup>2</sup>	(/catathelasma)	Agaricales (Basidiomycota)	E	No data	Arnolds (1995)
<i>Choiromyces</i> <sup>3</sup>	/tuber-helvella	Pezizales (Ascomycota)	E	C <sup>5</sup>	Arnolds (1995)
<i>Chroogomphus</i> <sup>2</sup>	/suillus-rhizopogon	Boletales (Basidiomycota)	E	C, S	Arnolds (1995)
<i>Clavariadelphus</i> <sup>4</sup>	/clavariadelphus	Gomphales (Basidiomycota)	E	No data	Arora (1986)
<i>Clavulina</i>	/clavulina	Cantharellales (Basidiomycota)	E	S or Mf	Arora (1986), Ma et al. (2010)
<i>Cortinarius</i> (incl. <i>Rozites</i> and <i>Dermocybe</i> ) <sup>1,3</sup>	/cortinarius	Agaricales (Basidiomycota)	E	S, Mf, Ms	Arora (1986)
<i>Craterellus</i>	/cantharellus	Cantharellales (Basidiomycota)	\$	Ms	Arnolds (1995)
<i>Cystangium</i> <sup>2,3</sup>	/russula-lactarius	Russulales (Basidiomycota)	E	C, S, Ms <sup>5</sup>	Trappe personal communication
<i>Entoloma s. str.</i> <sup>3,4</sup>	/entoloma	Agaricales (Basidiomycota)	E	Mf	Co-david et al. (2009)
<i>Fistulinella</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Gastroboletus</i> <sup>3</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Trappe et al. (2007)

<i>Gautieria</i> <sup>3</sup>	/ramaria-gautieria	Gomphales (Basidiomycota)	E	Mm	Trappe et al. (2007)
<i>Genea</i> <sup>3</sup>	/genea-humaria	Pezizales (Ascomycota)	E	S	Trappe et al. (2007)
<i>Geopora</i> <sup>3</sup>	/geopora	Pezizales (Ascomycota)	E	S	Trappe et al. (2007)
<i>Gomphidius</i>	/suillus-rhizopogon	Boletales (Basidiomycota)	E	Ms	Arnolds (1995)
<i>Gomphus</i>	/ramaria-gautieria	Gomphales (Basidiomycota)	E	Mm	Arora Perez-Moreno et al. (2008)
<i>Gymnomycetes</i> <sup>3</sup>	/russula-lactarius	Russulales (Basidiomycota)	E	C, S, Ms <sup>5</sup>	Trappe personal communication
<i>Gyrodon s. stricto</i>	/paxillus-gyrodon	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Gyroporus</i>	/pisolithus-scleroderma	Boletales (Basidiomycota)	E	L <sup>5</sup>	Arora (1986)
<i>Hebeloma</i>	/hebeloma-ainicola	Agaricales (Basidiomycota)	E	Mf	Perez-Moreno et al. (2008)
<i>Heimioporus</i> (syn. <i>Heimiella</i> )	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Helvella</i>	/tuber-helvella	Pezizales (Ascomycota)	E	C	Arora (1986), Perez-Moreno et al. (2008)
<i>Hydnотrya</i> <sup>3</sup>	/hydnotrya	Pezizales (Ascomycota)	E	C	Trappe et al. (2007)
<i>Hydnum</i>	/cantharellus	Cantharellales (Basidiomycota)	E	Mf	Arnolds (1995)
<i>Hygrophorus</i>	/hygrophorus	Agaricales (Basidiomycota)	E	C	Arnolds (1995), Perez-Moreno et al. (2008)
<i>Hysterangium</i>	/hysterangium	Hysterangiales (Basidiomycota)	E	Mm	Trappe et al. (2007)
<i>Inaia</i> <sup>2,3</sup>	/leucangium	Pezizales (Ascomycota)	\$	No data	Trappe et al. (2007)
<i>Inocybe</i> <sup>1,3</sup>	/inocybe	Agaricales (Basidiomycota)	E	S	Kuyper (1986)
<i>Kalapiya</i> <sup>2,3</sup>	/leucangium	Pezizales (Ascomycota)	E	No data	Trappe et al. (2010)
<i>Laccaria</i> <sup>3</sup>	/laccaria	Agaricales (Basidiomycota)	E	Mf	Bessette et al. (1997), Arora (1986)
<i>Lactarius</i>	/russula-lactarius	Russulales (Basidiomycota)	\$	C, S, Ms	Arora (1986)
<i>Leccinellum</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Boa (2004)
<i>Leccinum</i>	/boletus	Boletales (Basidiomycota)	\$	L	Arnolds (1995)
<i>Leucangium</i> <sup>3</sup>	/leucangium	Pezizales (Ascomycota)	\$	C	Trappe et al. (2007)

(continued)

Table 2.1 (continued)

Genus	EM lineage	Order (Phylum)	Edibility	Ectomycorrhizal exploration type	References
<i>Lyophyllum</i> <sup>4</sup>	/paralytophyllum	Agaricales (Basidiomycota)	E	Mf	Perez-Moreno et al. (2008), Yamada et al. (2001)
<i>Macowanites</i> <sup>3</sup>	/russula-lactarius	Russulales (Basidiomycota)	E	C, S, Ms <sup>5</sup>	Trappe personal communication
<i>Melanogaster</i> <sup>3</sup>	/paxillus-gyrodon	Boletales (Basidiomycota)	E	L	Trappe et al. (2007), Pena et al. (2010)
<i>Mycoclelandia</i> <sup>2,3</sup>	/terfezia-peziza depressa	Pezizales (Ascomycota)	E	C <sup>5</sup>	Trappe et al. (2008)
<i>Otidea</i> <sup>3</sup>	/otidea	Pezizales (Ascomycota)	E	S	Arnolds (1995);
<i>Phylloporus</i>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Arora (1986)
<i>Picoa</i> <sup>3</sup>	/geopora	Pezizales (Ascomycota)	E	S	Arora (1986), Alsheikh and Trappe (1983)
<i>Polyozellus</i> <sup>2</sup>	/pseudotomentella	Thelephorales (Basidiomycota)	E	No data	Pilz et al. (2003)
<i>Porphyrellus</i>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Boa (2004)
<i>Pseudoboletus</i>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Pulveroboletus</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Boa (2004)
<i>Ramaria</i> <sup>4</sup>	/ramaria-gautieria	Gomphales (Basidiomycota)	E	Mm	Perez-Moreno et al. (2008)
<i>Reddellomyces</i> <sup>3</sup>	/tuber-helvella	Pezizales (Ascomycota)	E	C <sup>5</sup>	Trappe et al. (2008)
<i>Retiboletus</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Rhizopogon</i> <sup>3</sup>	/suillus-rhizopogon	Boletales (Basidiomycota)	E	L	Visnovsky et al. (2010)
<i>Rubinoboletus</i> <sup>2</sup>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Boa (2004)
<i>Russula</i>	/russula-lactarius	Russulales (Basidiomycota)	\$	C, S, Ms	Arnolds (1995)
<i>Sarcodon</i>	/hydnellum-sarcodon	Thelephorales (Basidiomycota)	E	Mm	Arnolds (1995), Barros et al. (2007)
<i>Scleroderma</i> <sup>3</sup>	/pisolithus-scleroderma	Boletales (Basidiomycota)	E	L	Boa (2004)
<i>Srobilomyces</i>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Arora (1986)
<i>Suillus</i> <sup>3</sup>	/suillus-rhizopogon	Boletales (Basidiomycota)	E	L	Arnolds (1995)
<i>Terfezia s. stricto</i> <sup>3</sup>	/terfezia-peziza depressa	Pezizales (Ascomycota)	\$	C <sup>5</sup>	Díez et al. (2002)
<i>Thelephora</i>	/tomentella-thelephora	Thelephorales (Basidiomycota)	\$	Ms	Sha et al. (2008)
<i>Tirmania</i> <sup>3</sup>	/terfezia-peziza depressa	Pezizales (Ascomycota)	\$	C <sup>5</sup>	Díez et al. (2002)

<i>Tremellodendron</i>	/sebacina	Sebacinales (Basidiomycota)	E	S <sup>5</sup>	Bessette et al. (1997), Pena et al. (2010)
<i>Tricholoma</i>	/tricholoma	Agaricales (Basidiomycota)	\$	Mf, Ms, L	Arnolds (1995)
<i>Truncocolumella</i> <sup>3</sup>	/suillus-rhizopogon	Boletales (Basidiomycota)	E	L	Trappe et al. (2007)
<i>Tuber</i> <sup>3</sup>	/tuber-helvella	Pezizales (Ascomycota)	\$	C	Arora (1986), Trappe et al. (2007)
<i>Turbinellus</i>	/ramaria-gautieria	Gomphales (Basidiomycota)	E	Mm <sup>5</sup>	Arora (1986) [as <i>Gomphus</i> spp.]
<i>Tylopius</i>	/boletus	Boletales (Basidiomycota)	E	L	Arora (1986)
<i>Ulluria</i> <sup>2,3</sup>	/terfezia-peziza depressa	Pezizales (Ascomycota)	E	C <sup>5</sup>	Trappe et al. (2008)
<i>Xanthoconium</i>	/boletus	Boletales (Basidiomycota)	E	L <sup>5</sup>	Bessette et al. (2000)
<i>Xerocomus</i>	/boletus	Boletales (Basidiomycota)	E	L	Arora (1986)
<i>Zelleromyces</i> <sup>3</sup>	/russula-lactarius	Russulales (Basidiomycota)	E	C, S, Ms <sup>5</sup>	Trappe et al. (2007)

Genera with edible species are indicated by an E, whereas those with species considered choice edibles are indicated by a \$. Genera known to contain both edible species and deadly poisonous species are indicated by a 1, genera suspected but not proven to be ectomycorrhizal are indicated by a 2, genera with some or all sequestrate species are indicated by a 3, and genera known to be polyphyletic with only some ectomycorrhizal species are indicated by a 4. Ectomycorrhizal exploration strategies are designated according to the classifications of Agerer (2001) as follows: contact (C), short distance (S), medium-distance smooth (Ms), medium-distance fringe (Mf), medium-distance mat (Mm), and long distance (L). Genera where the ectomycorrhizal exploration strategy was inferred based on the phylogenetic relationships in addition to data from related species are indicated by a 5

times, the EM habit is now known to have arisen independently in at least 66 different fungal lineages (Tedersoo et al. 2010). Given the multiple independent origins of the EM habit, it is likely that selection pressures and adaptations leading to the symbiosis were different for the various phylogenetic lineages. We expect that the similar EM structures that are common across the different lineages (e.g., the hyphal sheath and Hartig net) probably mask large functional differences between different EM fungal groups.

Fungal molecular systematics studies have also repeatedly shown that the morphology of fruiting structures is a highly plastic trait and that similar fruiting body plans have evolved many times in different EM fungal groups. For example, “agaricoid” fruiting bodies with a stipe and gills have arisen independently in the Agaricales (e.g., *Amanita*), Russulales (e.g., *Lactarius*), Boletales (e.g., *Phylloporus*), Gomphales (e.g., *Gomphus*), and Cantharellales (e.g., *Cantharellus*), whereas “coralloid” forms can be found in Gomphales (e.g., *Ramaria*) and Cantharellales (e.g., *Clavulina*). Similarly, the sequestrate, truffle-like fruiting body plan has arisen independently many different times and is present in at least 94 different genera of EM fungi (Tedersoo et al. 2010). These exciting discoveries have been paramount for understanding fungal evolution but have caused massive and rapid reorganizations in fungal taxonomy (Hibbett 2007).

## 2.3 The Lineage Concept

In one of the first large-scale assessments of evolutionary relationships of euagarics (mushrooms), Moncalvo et al. (2002) established an informal, rank-free nomenclature for discussing monophyletic groups of any taxonomic level. In their notation system, the monophyletic lineage name is written in non-italicized lowercase letters and preceded with the symbol “/” (e.g., /*amanita*). The lineage-based concept is informal and therefore mediates some of the problems that arise due to polyphyly (e.g., multiple taxa with the same genus name are dispersed in multiple different lineages) and due to phylogenetic uncertainty (e.g., we sometimes know which genera belong to a particular lineage, but we do not always know how they are related to each other within that lineage).

### 2.3.1 Lineages of EM Fungi

A similar lineage-based concept was adopted by Tedersoo et al. (2010) in a recent review of global patterns of biogeography and evolution of EM fungi. Tedersoo et al. (2010) identified 66 monophyletic groups of EM fungi in the Ascomycota, Basidiomycota, and Zygomycota with different ages, diversity levels, and global distributions.

In this chapter, we use the same organizational concept of the rank-free EM lineages as Tedersoo et al. (2010) to examine the biology and ecology of the edible EM fungi within this framework. Specifically, we examine which EM lineages contain edible fungi and how many genera within each lineage are considered to have edible species. We also explore what is known about the systematics, ecology, and life-history traits of EM lineages that have edible species. Based on our findings, we suggest ways in which phylogenetic knowledge of the EM lineages can inform future decisions on how to best manage EM ecosystems for edible fungi.

Throughout this chapter, we assume that species traits are phylogenetically conserved, meaning that closely related species are more likely to be similar in terms of their biology and ecology than are more distantly related species (Felsenstein 1985). This is known to be true of EM fungi for many ecological, physiological, and morphological traits (Agerer 2006; Smith and Read 2008).

### 2.3.2 Lineages of EEMM

Currently, 66 unique lineages of EM fungi that belong to 15 orders of fungi are recognized (Tedersoo et al. 2010), but only 34 of these lineages contain species that produce edible sporocarps (Table 2.1). We define edible fungi as those species that are regularly consumed in at least one part of the world. Some EM fungi may be considered a delicacy in one country, but not consumed elsewhere (e.g., some species of *Thelephora* are a regularly eaten specialty in China but only rarely eaten in other parts of the world). Edible EM fungi are currently placed in eight orders: Agaricales, Boletales, Cantharellales, Gomphales, Hysterangiales, Pezizales, Russulales, and Thelephorales. Some of these orders contain a large number of edible species (e.g., Agaricales, Boletales, Pezizales), but taxonomic knowledge gaps prevent us from making reliable estimates of the true number of edible species at this time. We have relatively good information for economically important genera that have been recently studied (e.g., *Tuber*—see Jeandroz et al. 2008, Bonito et al. 2012), but many genera and lineages remain poorly known (e.g., *Clavulina*—see Henkel et al. 2011).

Although it is difficult to make definitive statements about the number of edible species within all EM fungi lineages, we are better able to assess the distribution of edibles at the genus level. By our estimation, there are 82 genera of EM fungi that contain at least one edible species. The majority of these genera belong to the *Basidiomycota* (64 genera), whereas fewer belong to *Ascomycota* (18 genera) (Table 2.1). Many of the 66 lineages contain edible species in only one genus (e.g., *Amanita*, *Genea*, *Hygrophorus*, *Hysterangium*), but others, such as the */boletus*, */tuber-helvella*, */russula-lactarius*, */suillus-rhizopogon* lineages, contain many genera with edible species. Enumerating edible EM fungi at the genus level is insufficient to give us a complete understanding of the diversity of edibles within each lineage, but it is a useful starting point that highlights the serious need for more taxonomic work in many groups.

The phylogeny in Fig. 2.1 depicts our current understanding of how the different EM fungal lineages that contain edible species are related to one another. This figure visually highlights some key relationships: (1) a high number of lineages with edible species are *not* closely related to one another; (2) Basidiomycota constitute the majority of the lineages having edible fruiting bodies; (3) edible EM taxa are particularly concentrated within the Agaricales, Boletales, and Pezizales; (4) the Agaricales includes the largest number of distinct EM lineages with edible species; (5) the /boletus lineage has the greatest number of genera with edible species; and (6) the relationships among some key groups are not yet well resolved (e.g., Thelephorales, Cantharellales).

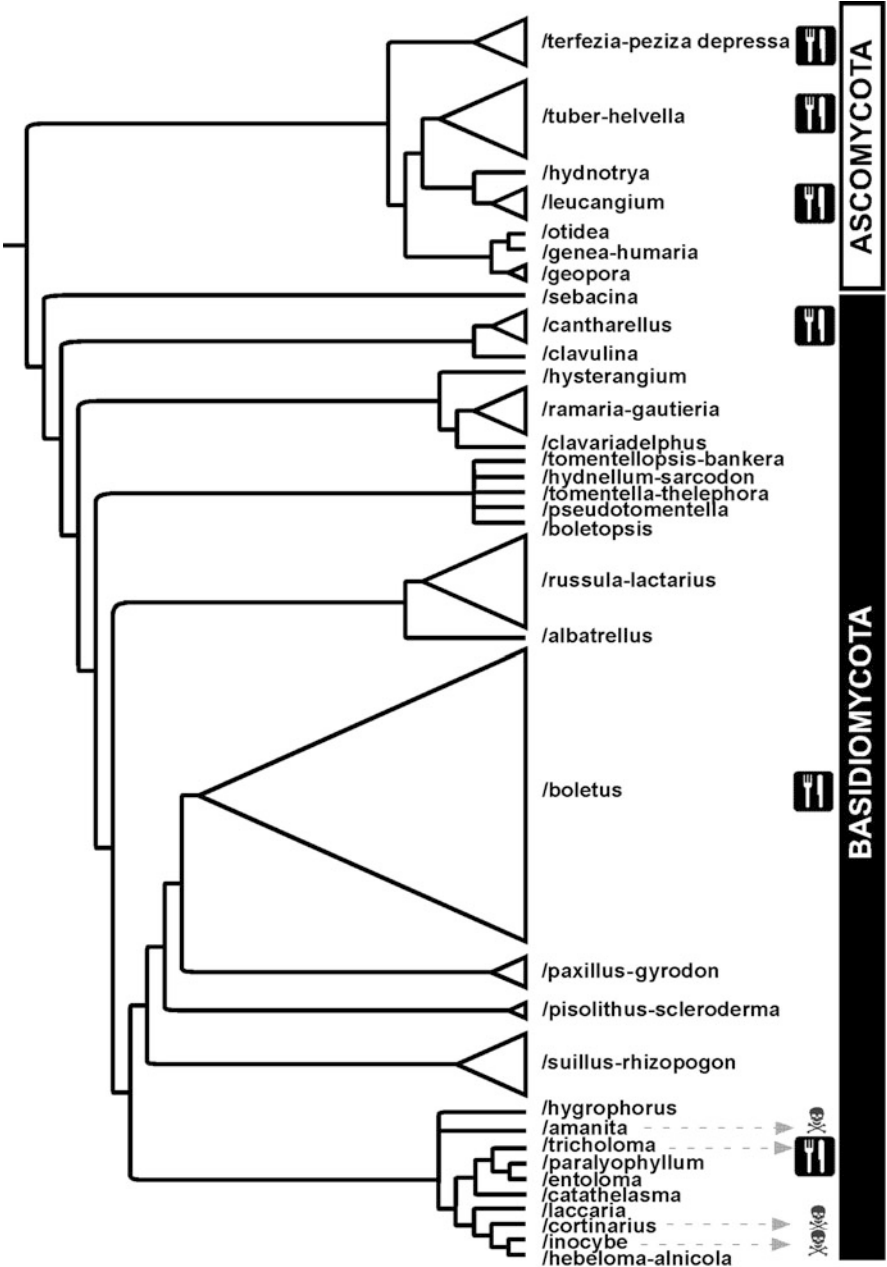
## 2.4 Biology of EM Fungi

Given the estimated 400 million years of divergence between the Ascomycota and Basidiomycota (Taylor and Berbee 2006), we expect members of these two phyla to differ significantly in terms of their biology and life cycle.

### 2.4.1 Biology of the Ascomycota

Although the EM Ascomycota belong to many orders (including Eurotiales, Sordariales, and Helotiales), all of the edible EM Ascomycota belong to the Pezizales (Table 2.1). Many of the seven different EM Pezizales lineages with edible sporocarps appear to have evolved from pyrophilic ancestors or humus saprobes. Most are adapted to disturbed habitats, drought-prone environments, and fire. Biotrophic Pezizales are not thought to produce lignin-degrading enzymes, and most EM Pezizales appear poorly adapted for growth on wood or other heavily lignified substrates (Egger 1986). EM Pezizales do, however, grow well in mineral soils with low organic content and with a pH > 7.0 (Bonito et al. 2012).

Ascomycota spend most of their lives as haploids (1 n); they can simply germinate from spores and begin active growth and EM formation as functional individuals (Bonito et al. 2012). Many of the EM Pezizales also produce conidia, although the dispersal and/or mating functions of these asexual propagules have not yet been shown (Urban et al. 2004; Healy, Smith and Bonito unpublished). Despite the fact that they evolved separately from one another, the edible EM Ascomycota appear to share a similar, yet not completely understood, mating biology (Varda Kagan-Zur and Roth-Bejerano 2008). They are characterized by the maintenance of two mating idiomorphs (1-1-1 and 1-2-1) and are thought to reproduce through heterokaryotic mating as detailed by Rubini et al. in Chap. 4. However, the number of species and lineages that have been studied is still small, and recent studies of species in the /terfezia-peziza depressa lineage indicate that there may be exceptions to these patterns (Varda Kagan-Zur and Roth-Bejerano 2008).



**Fig. 2.1** Cladogram depicting the relationships between lineages of ectomycorrhizal (EM) fungi containing edible species. The size of the *triangle* scales to the number of genera in each lineage that contains edible species. Those lineages that also contain deadly species are depicted by the *skull and crossbones* symbol (e.g., *Amanita phalloides* (Vaill. Ex Fr.) Link; *Inocybe erubescens* Blytt; *Cortinarius orellanus* Fr.). The *dinner plate* symbol marks the three lineages of Ascomycota and Basidiomycota that contain the most sought-after and valuable species

All of the known pezizalean EM fungi that have been studied to date produce short-distance or contact-type ectomycorrhizas where their hyphae and cystidia grow close to plant roots. No Pezizales EM fungi are known to produce rhizomorphs, hyphal cords, or hyphal mats (Table 2.1). We hypothesize that the haploid life cycles of these EM Pezizales and their postfire evolutionary history preadapt these fungi for colonizing via spores. These traits also help to explain their success in tolerating, and at times flourishing, in disturbed habitats.

### 2.4.2 *Biology of the Basidiomycota*

In sharp contrast to Ascomycota, Basidiomycota EM are highly diverse in their mating biology, habitat preferences, and evolutionary histories. Most Basidiomycota produce haploid spores that must germinate and then presumably fuse with another haploid to form a dikaryon (prior to initiating ectomycorrhizas) (Horton 2006). Most EM basidiomycetes germinate in the presence of host plant roots, although germination rates are usually low and only select species are efficient at colonizing roots via spores (Ishida et al. 2008). These traits effectively limit the dispersal abilities of many EM Basidiomycota to within a few meters of a parental sporocarp (Li 2005). Exceptional basidiomycete species that establish well from spores have one or a few traits in common: they routinely produce multinucleate spores (e.g., *Laccaria* spp.), they have spores that are deposited *en mass* via animal mycophagy (e.g., *Rhizopogon* spp.), and/or they have good saprotrophic abilities (e.g., *Hebeloma* spp.) (Horton 2006; Ishida et al. 2008; Kawai et al. 2008).

The Basidiomycota EM lineages also share the important common trait that they appear to have evolved from wood or humus saprobes (Tedersoo et al. 2010). Unlike the pezizalean EM fungi, many (but certainly not all) EM basidiomycetes grow well in acidic soils with high organic matter content. Many EM basidiomycetes (including species in the /cortinarius, /hygrophorus, /ramaria-gautieria, and /russula-lactarius lineages) have been shown to produce lignin-degrading peroxidases (Bodeker et al. 2009) and also appear capable of degrading woody substrates. Although most basidiomycetes probably retain at least some wood-degrading capabilities, they exhibit a wide degree of variation in their dependence on host plants. Members of some genera are readily cultured on artificial media away from their host plants (e.g., species of *Laccaria*, *Hebeloma*, and *Suillus*), whereas members of other genera either have never been successfully propagated or die in pure culture or when transferred (e.g., species of *Tremellodendron* and *Inocybe*) (Iotti et al. 2005). Certain taxa may grow better on particular types of culture media (see Chap. 9).

As with Basidiomycota in general, the distantly related EM lineages likely exhibit wide diversity in their mating biology (Kües et al. 2011). However, because of the difficulties in germinating EM basidiospores and with culturing EM fungi in general (Ali and Jackson 1988), relatively few species have been studied in detail. The genus *Laccaria* has served as a model for studies of mating in EM fungi. Thus, we know that *Laccaria bicolor* (Maire) PD Orton has a tetrapolar mating system

with ca. 45 different mating types (Raffle et al. 1995; Niculita-Hirzel et al. 2008). In contrast, *Rhizopogon rubescens* Tul. and C. Tul. and several *Suillus* species have been shown to have bipolar mating systems (Fries and Sun 1992; Kawai et al. 2008). Unlike members of the Ascomycota, it is assumed that EM Basidiomycota generally do not produce asexual spores (e.g., anamorphs), based on evidence from in vitro culture studies (Hutchison 1989).

In contrast to the uniformly short-distance EM exploration types of the Ascomycota, the EM Basidiomycota exhibit a very wide variation in the morphology of the hyphae that emerge from ectomycorrhizas to explore for nutrients and roots to colonize. These exploration types range from contact or short-distance types for many species in the /hyrophorus, /inocybe, /clavulina, /sebacina, and /russula-lactarius lineages to the long-distance and/or tuberculate EM types in /bankera and in *Boletales* lineages (e.g., the /boletus, /pisolithus-scleroderma, /suillus-rhizopogon, and /paxillus-gyrodon lineages) (Agerer 2006). Several groups within Boletales have also been shown to regularly form sclerotia, although the biological function of these structures in relation to EM ecology is not known (Smith and Pfister 2009). Several basidiomycete EM lineages form extensive hyphal mats that are accompanied by mat-type EM formations (see Table 2.1; Dunham et al. 2007). Many of these extensively ramified EM systems are associated with highly organized rhizomorphs to less extensive hyphal cords.

## 2.5 Future Research and Management

### 2.5.1 Taxonomic Uncertainties

The exact number of EEMM species is not known at this time. This is due partly to the lack of taxonomic studies from certain parts of the world (e.g., West Africa, Southeast Asia) and also due to the large number of species complexes that still are in need of further study (e.g., *Boletus edulis* Bull.) (Dentinger et al. 2010). Basic taxonomic studies, coupled with complementary molecular data, will help to determine a realistic estimate of the number of edible EM fungal species. It is worthy to note how in even the most economically important fungal groups and in those with significant cultural value, true species diversity is unknown and underestimated. Prominent examples of this include the recent descriptions of several new choice edible species from well-studied regions of the Western USA (e.g., *Boletus rex-veris* D. Arora and Simonini, *B. regineus* D. Arora and Simonini, and *Cantharellus californicus* Arora and Dunham and *Cantharellus cascadenis* Dunham, O'Dell, and R. Molina) (Dunham et al. 2003; Arora 2008; Arora and Dunham 2008). In some cases, taxonomic uncertainties extend to generic level or higher. Genera such as *Entoloma*, *Amanita*, and *Lyophyllum* currently include both EM and saprotrophic edible mushroom species, making it difficult to enumerate the number of species with each of the different trophic modes (Tedersoo et al. 2010).

## 2.5.2 Management of EEM Fungi

Management decisions regarding EEMM should be influenced by knowledge of both the natural and evolutionary history of the particular EM species. Because lineages of EEMM are the result of evolutionary changes through an act of independent sequential events, these lineages are shaped by a range of varying selective factors. Coincidentally, management strategies are expected to differ significantly between taxa and lineages. For example, the management of boletes belonging to the Basidiomycota may promote organic matter and soil acidity, while management of truffles belonging to the Ascomycota would generally avoid such conditions. Likewise, pioneer species that depend heavily on spores for dispersal require different management regimes than fungi that are sensitive to disturbance or better adapted for root colonization via mycelial spread (Peay et al. 2011).

### 2.5.2.1 Cultivated EM Fungi

It is interesting to note that species from only seven of the 34 EM fungal lineages with edible species have been cultivated (in some cases, by accident). These lineages include /*tuber-helvella* (see Chaps. 10, 11, 12 and 13), /*terfezia* (see Chap. 14), /*cantharellus* (Danell and Camacho 1997), /*russula-lactarius* (see Chap. 16), /*suillus-rhizopogon* (see Chap. 16), /*tricholoma* (see Chap. 16), and /*laccaria* (DiBattista et al. 1996). By far, the greatest successes in the cultivation of edible EM fungi have been with truffle fungi and *Tuber* in particular. Truffle fungi generally grow slowly in culture, but their spores can readily infect plant roots (see Chap. 9). Current cultivation practices start with the use of spore inoculum on appropriate host plant seedling roots, followed by outplanting, proper irrigation, and appropriate soil amendments (Le Tacon et al. 1982). Adapting similar approaches for basidiomycete mushrooms has proved extremely challenging for most edible EM. Despite the fact that many of these basidiomycete mushrooms grow readily in pure culture, their spores are generally not as effective in directly establishing ectomycorrhizas. Consequently, mycelium-based techniques for inoculating trees continue to be developed and improved for many edible EM basidiomycete mushrooms but also ascomycetes (Rossi et al. 2007). When inoculating seedlings with basidiomycete mycelium, it is important to use a mated, dikaryotic strain (such as that which arises from the vegetative tissue of a fruiting body) to ensure that fruiting is possible. Once introduced, specific genotypes can persist for years to decades (Henrion et al. 1994), depending on site conditions and the competitiveness of the given species on EM roots. Strategies for limiting competitive exclusion are also important. This can be done by introducing species where they are most competitive (e.g., within their natural range), by introducing them in areas with limited competition (e.g., enemy-release hypothesis) or by soil modification processes that reduce propagules and competitiveness of non-target taxa.

Future successes in EEMM domestication will likely include pioneer species adapted to disturbed habitats and EEMM species that can readily be cultured or inoculated onto roots via spores or mycelium. Pioneer EM fungi are adapted to grow well in younger aged and managed stands (e.g., tree plantations). Similar to how many animals have still not been domesticated even after many attempts certain lineages of EM fungi are probably not amenable to domestication, whereas others may be preadapted for domestication. Further studies are needed to ascertain the maturity conditions (how large an individual genet must be to initiate fruiting) and environmental cues that initiate the fruiting process in the different groups of fungi. Currently, the effect of genet size and diversity on fruiting body production and yield is unknown.

## 2.6 Conclusions

The majority of edible EM fungal lineages and species are currently only found in the wild. This includes many species of boletes, chanterelles, and even truffles (Wang and Hall 2004). Because nature provides the genetic resources for both cultivated and wild-collected EM species, policies that conserve natural habitats where these fungi grow and reproduce are critical. Strategies for simultaneously managing forests for both edible fungi and for timber have already been well articulated (Pilz and Molina 1996; Boa 2004; Trappe et al. 2009). Future research aimed at stimulating productivity and increasing yields from natural stands, and adaptive management approaches and refined techniques for habitat and niche modeling are needed to fully understand and conserve the diversity and productivity of EEMM (Molina et al. 2011).

**Acknowledgments** MS is grateful for financial support from the University of Florida's Institute of Food and Agricultural Sciences (IFAS). GB was supported through the Department of Energy, Office of Biological and Environmental Research, Genomic Science Program. Both authors would like to thank Eric Boa and Martin Ryberg for valuable input and feedback on this manuscript and Dr. James M. Trappe and Rytas Vilgalys for providing positive mentoring experiences.

## References

- Agerer R (2001) Exploration types of ectomycorrhizae: a proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza* 11:107–114
- Agerer R (2006) Fungal relationships and structural identity of their ectomycorrhizae. *Mycol Prog* 5:67–107. doi:[10.1007/s11557-006-0505-x](https://doi.org/10.1007/s11557-006-0505-x)
- Ali NA, Jackson RM (1988) Effects of plant-roots and their exudates on germination of spores of ectomycorrhizal fungi. *Trans Br Mycol Soc* 91:253–260
- Alsheikh M, Trappe JM (1983) Taxonomy of *Phaeangium lefebvrei*, a desert truffle eaten by birds. *Can J Bot* 61:1919–1925

- Arnolds E (1995) Conservation and management of natural populations of edible fungi. *Can J Bot* 73:987–998
- Arora D (1986) *Mushrooms demystified*. Ten Speed, Berkeley, CA, 959p
- Arora D (2008) California porcini: three new taxa, observations on their harvest, and the tragedy of no commons. *Econ Bot* 62:356–375. doi:[10.1007/s12231-008-9050-7](https://doi.org/10.1007/s12231-008-9050-7)
- Baar J, Ozinga WA, Kuyper TW (1994) Spatial-distribution of *Laccaria bicolor* genets reflected by sporocarps after removal of litter and humus layers in a *Pinus sylvestris* forest. *Mycol Res* 98:726–728
- Barros L, Ferreira M-J, Queirós B, Ferreira I, Baptista P (2007) Total phenols, ascorbic acid,  $\beta$ -carotene and lycopene in Portuguese wild edible mushrooms and their antioxidant activities. *Food Chem* 103:413–419. doi:[10.1016/j.foodchem.2006.07.038](https://doi.org/10.1016/j.foodchem.2006.07.038)
- Bessette AE, Bessette AR, Fischer DW (1997) *Mushrooms of northeastern North America*. Syracuse University Press, Syracuse, NY, 582p
- Bessette AE, Roody WC, Bessette AR (2000) *North American Boletes: a color guide to the fleshy pored mushrooms*. Syracuse University Press, Syracuse, NY, 400p
- Boa E (2004) Wild edible fungi—a global overview of their use and importance to people. Non-wood forest products, vol 17. Food and Agriculture Organization of the United Nations, Rome, p 143. <http://www.fao.org/docrep/007/y5489e/y5489e00.htm>
- Bodeker ITM, Nygren CMR, Taylor AFS, Olson A, Lindahl BD (2009) Class II peroxidase-encoding genes are present in a phylogenetically wide range of ectomycorrhizal fungi. *ISME J* 3:1387–1395. doi:[10.1038/ismej.2009.77](https://doi.org/10.1038/ismej.2009.77)
- Bonito G, Smith M, Brennenman T, Vilgalys R (2012) Assessing ectomycorrhizal fungal spore banks of truffle producing soils with pecan seedling trap-plants. *Plant Soil* 356:357–366. doi:[10.1007/s11104-012-1127-5](https://doi.org/10.1007/s11104-012-1127-5)
- Brundrett M (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant Soil* 320:37–77. doi:[10.1007/s11104-008-9877-9](https://doi.org/10.1007/s11104-008-9877-9)
- Brundrett MC, Kendrick B (1987) The relationship between the ash bolete (*Boletinus merulioides*) and an aphid parasitic on ash tree roots. *Symbiosis* 3:315–320
- Bruns TD, Fogel R, White TJ, Palmer JD (1989) Accelerated evolution of a false-truffle from a mushroom ancestor. *Nature* 339:140–142
- Chopra R (1933) *Indigenous drugs of India: their scientific cultivation and manufacture, with numerous suggestions intended for educationists and capitalists*. Academic Publishers, Kolkata
- Co-David D, Langeveld D, Noordeloos ME (2009) Molecular phylogeny and spore evolution of Entolomataceae. *Persoonia* 23:147–176
- Dahlstrom JL, Smith JE, Weber NS (2000) Mycorrhiza-like interaction by *Morchella* with species of the Pinaceae in pure culture synthesis. *Mycorrhiza* 9:279–285
- Danell E, Camacho FJ (1997) Successful cultivation of the golden chanterelle. *Nature* 385:303
- Dentinger BTM, Ammirati JF, Both EE, Desjardin DE, Halling RE, Henkel TW, Moreau PA, Nagasawa E, Soyong K, Taylor AF, Watling R, Moncalvo JM, McLaughlin DJ (2010) Molecular phylogenetics of porcini mushrooms (*Boletus* section *boletus*). *Mol Phylogenet Evol* 57:1276–1292. doi:[10.1016/j.ympev.2010.10.004](https://doi.org/10.1016/j.ympev.2010.10.004)
- Díaz G, Carrillo C, Honrubia M (2009) Production of *Pinus halepensis* seedlings inoculated with the edible fungus *Lactarius deliciosus* under nursery conditions. *New For* 38:215–227. doi:[10.1007/s11056-009-9142-y](https://doi.org/10.1007/s11056-009-9142-y)
- DiBattista C, Selsos MA, Bouchard D, Stenstrom E, Le Tacon F (1996) Variations in symbiotic efficiency, phenotypic characters and ploidy level among different isolates of the ectomycorrhizal basidiomycete *Laccaria bicolor* strain s 238. *Mycol Res* 100:1315–1324
- Díez J, Manjón JL, Martín F (2002) Molecular phylogeny of the mycorrhizal desert truffles (Terfezia and Tirmania), host specificity and edaphic tolerance. *Mycologia* 94:247–259
- Douhan GW, Vincenot L, Gryta H, Selsos MA (2011) Population genetics of ectomycorrhizal fungi: from current knowledge to emerging directions. *Fungal Biol* 115:569–597. doi:[10.1016/j.funbio.2011.03.005](https://doi.org/10.1016/j.funbio.2011.03.005)

- Dunham S, Arora D (2008) A new commercially valuable chanterelle species, *Cantharellus californicus* sp. nov., associated with live oak in California, USA. *Econ Bot* 62:376–391. doi:[10.1007/s12231-008-9042-7](https://doi.org/10.1007/s12231-008-9042-7)
- Dunham SM, Larsson KH, Spatafora JW (2007) Species richness and community composition of mat-forming ectomycorrhizal fungi in old- and second-growth Douglas fir forests of the HJ Andrews Experimental Forest Oregon, USA. *Mycorrhiza* 17:633–645. doi:[10.1007/s00572-007-0141-6](https://doi.org/10.1007/s00572-007-0141-6)
- Egger KN (1986) Substrate hydrolysis patterns of post-fire ascomycetes (pezizales). *Mycologia* 78:771–780
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15
- Frank B (2005) On the nutritional dependence of certain trees on root symbiosis with below-ground fungi (an English translation of A.B. Frank's classic paper of 1885). *Mycorrhiza* 15: 267–275
- Fries N, Sun Y-P (1992) The mating system of *Suillus bovinus*. *Mycol Res* 96:237–238
- Gardes M, Bruns T (1996) Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: minimal overlap between the mature forest and resistant propagule communities. *Can J Bot* 8:1837–1850. doi:[10.1046/j.1365-294x.1999.00773.x](https://doi.org/10.1046/j.1365-294x.1999.00773.x)
- Hall IR, Brown GT, Zambonelli A (2007) Taming the truffle—the history, lore and science of the ultimate mushroom. Timber, Portland, OR
- Henkel T, Aime M, Chin M, Andrew C (2004) Edible mushrooms from Guyana. *Mycologist* 18:104–111
- Henkel TW, Aime MC, Uehling JK, Smith ME (2011) New species and distribution records of *Clavulina* (Cantharellales, Basidiomycota) from the Guiana Shield. *Mycologia* 103:883–894. doi:[10.3852/11-130](https://doi.org/10.3852/11-130)
- Henrion B, Dibattista C, Bouchard D, Vairelles D, Thompson BD, Letacon F, Martin F (1994) Monitoring the persistence of *Laccaria bicolor* as an ectomycorrhizal symbiont of nursery-grown Douglas-fir by PCR of the rDNA intergenic spacer. *Mol Ecol* 3:571–580
- Hibbett DS (2007) After the gold rush, or before the flood? Evolutionary morphology of mushroom-forming fungi (Agaricomycetes) in the early 21st century. *Mycol Res* 111:1001–1018. doi:[10.1016/j.mycres.2007.01.012](https://doi.org/10.1016/j.mycres.2007.01.012)
- Horton TR (2002) Molecular approaches to ectomycorrhizal diversity studies: variation in its at a local scale. *Plant Soil* 244:29–39
- Horton TR (2006) The number of nuclei in basidiospores of 63 species of ectomycorrhizal homobasidiomycetes. *Mycologia* 98:233–238. doi:[10.3852/mycologia.98.2.233](https://doi.org/10.3852/mycologia.98.2.233)
- Horton T, Bruns T (2001) The molecular revolution in ectomycorrhizal ecology: peeking into the black box. *Mol Ecol* 10:1855–1871. doi:[10.1046/j.0962-1083.2001.01333.x](https://doi.org/10.1046/j.0962-1083.2001.01333.x)
- Hutchison L (1989) Absence of conidia as a morphological character in ectomycorrhizal fungi. *Mycologia* 81:587–594
- Iotti M, Barbieri E, Stocchi V, Zambonelli A (2005) Morphological and molecular characterisation of mycelia of ectomycorrhizal fungi in pure culture. *Fungal Divers* 19:51–68
- Ishida TA, Nara K, Tanaka M, Kinoshita A, Hogetsu T (2008) Germination and infectivity of ectomycorrhizal fungal spores in relation to their ecological traits during primary succession. *New Phytol* 180:491–500. doi:[10.1111/j.1469-8137.2008.02572.x](https://doi.org/10.1111/j.1469-8137.2008.02572.x)
- Jacobson KM, Miller OK, Turner BJ (1993) Randomly amplified polymorphic DNA markers are superior to somatic incompatibility tests for discriminating genotypes in natural populations of the ectomycorrhizal fungus *Suillus granulatus*. *Proc Natl Acad Sci USA* 90:9159–9163
- James TY, Kauff F, Schoch CL, Matheny PB, Hofstetter V, Cox CJ, Celio G, Gueidan C, Fraker E, Miadlikowska J, Lumbsch HT, Rauhut A, Reeb V, Arnold AE, Amtoft A, Stajich JE, Hosaka K, Sung GH, Johnson D, O'Rourke B, Crockett M, Binder M, Curtis JM, Slot JC, Wang Z, Wilson AW, Schussler A, Longcore JE, O'Donnell K, Mozley-Standridge S, Porter D, Letcher PM, Powell MJ, Taylor JW, White MM, Griffith GW, Davies DR, Humber RA, Morton JB, Sugiyama J, Rossman AY, Rogers JD, Pfister DH, Hewitt D, Hansen K, Hambleton S, Shoemaker RA, Kohlmeyer J, Volkmann-Kohlmeyer B, Spotts RA, Serdani M, Crous PW,

- Hughes KW, Matsuura K, Langer E, Langer G, Untereiner WA, Lucking R, Budel B, Geiser DM, Aptroot A, Diederich P, Schmitt I, Schultz M, Yahr R, Hibbett DS, Lutzoni F, McLaughlin DJ, Spatafora JW, Vilgalys R (2006) Reconstructing the early evolution of fungi using a six-gene phylogeny. *Nature* 443:818–822. doi:[10.1038/nature05110](https://doi.org/10.1038/nature05110)
- Jeandroz S, Murat C, Wang YJ, Bonfante P, Le Tacon F (2008) Molecular phylogeny and historical biogeography of the genus *Tuber* the ‘true truffles’. *J Biogeogr* 35:815–829. doi:[10.1111/j.1365-2699.2007.01851.x](https://doi.org/10.1111/j.1365-2699.2007.01851.x)
- Kawai M, Yamahara M, Ohta A (2008) Bipolar incompatibility system of an ectomycorrhizal basidiomycete, *Rhizopogon rubescens*. *Mycorrhiza* 18:205–210. doi:[10.1007/s00572-008-0167-4](https://doi.org/10.1007/s00572-008-0167-4)
- Kretzer AM, Dunham S, Molina R, Spatafora JW (2005) Patterns of vegetative growth and gene flow in *Rhizopogon vinicolor* and *R. vesiculosus* (Boletales, Basidiomycota). *Mol Ecol* 14:2259–2268
- Kües U, James TY, Heitman J (2011) Mating type in basidiomycetes: unipolar, bipolar, and tetrapolar patterns of sexuality. *Mycota Evol Fungi Fungal Like Org* 14:97–160
- Kuyper TW (1986) A revision of the genus *Inocybe* in Europe. I. Subgenus *Inosperma* and the smooth-spored species of subgenus *Inocybe*. *Persoonia Suppl* 3:1–247
- Le Tacon F, Delmas J, Gleyze R, Bouchard D (1982) Effect of soil-water regime and fertilization on fructification of the black truffle of perigord (*Tuber melanosporum* Vitt.) in south east of France. *Acta Oecol* 3:291–306
- Li D-W (2005) Release and dispersal of basidiospores from *Amanita muscaria* var. *alba* and their infiltration into a residence. *Mycol Res* 109:1235–1242
- Lilleskov EA, Hobbie EA, Fahey TJ (2002) Ectomycorrhizal fungal taxa differing in response to nitrogen deposition also differ in pure culture organic nitrogen use and natural abundance of nitrogen isotopes. *New Phytol* 154:219–231
- Ma D, Yang G, Mu L (2010) Morphological and molecular analyses of ectomycorrhizal diversity in *Pinus densiflora* seedlings. *Symbiosis* 51:233. doi:[10.1007/s13199-010-0079-x](https://doi.org/10.1007/s13199-010-0079-x)
- Marx DH, Bryan WC (1970) Pure culture synthesis of ectomycorrhizae by *Thelephora terrestris* and *Pisolithus tinctorius* on different conifer hosts. *Can J Botany* 48:639–641
- Marx DH, Bryan WC, Cordell CE (1977) Survival and growth of pine seedlings with *Pisolithus ectomycorrhizae* after 2 years on reforestation sites in North Carolina and Florida. *Forest Sci* 23:363–373
- Melin E (1954) Growth factor requirements of mycorrhizal fungi of forest trees. *Svensk Bot Tidskr* 48:86–94
- Melin E, Krupa S (1971) Studies on ectomycorrhizae of Pine, II. Growth inhibition of mycorrhizal fungi by volatile organic constituents of *Pinus sylvestris* (scots pine) roots. *Physiol Plant* 25:337–338
- Miles P, Chang ST (2004) Mushrooms: cultivation, nutritional value, medicinal effect, and environmental impact. CRC, Boca Raton, FL
- Miller SL, Torres P, McClean TM (1994) Persistence of basidiospores and sclerotia of ectomycorrhizal fungi and *Morchella* in soil. *Mycologia* 86:89–95
- Molina R, Horton TR, Trappe JM, Marcot BG (2011) Addressing uncertainty: how to conserve and manage rare or little-known fungi. *Fungal Ecol* 4:134–146. doi:[10.1016/j.funeco.2010.06.003](https://doi.org/10.1016/j.funeco.2010.06.003)
- Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE, James TY, Aime MC, Hofstetter V, Verduin SJW, Larsson E, Baroni TJ, Thorn RG, Jacobsson S, Clemençon H, Miller OK (2002) One hundred and seventeen clades of euagarics. *Mol Phylogenet Evol* 23:357–400
- Morgan A (1995) Toads and toadstools: the natural history, folklore, and cultural oddities of a strange association. Celestial Arts, Berkeley, CA. ISBN 0-89087-777-7
- Niculita-Hirzel H, Labbe J, Kohler A, Le Tacon F, Martin F, Sanders IR, Kues U (2008) Gene organization of the mating type regions in the ectomycorrhizal fungus *Laccaria bicolor* reveals distinct evolution between the two mating type loci. *New Phytol* 180:329–342. doi:[10.1111/j.1469-8137.2008.02525.x](https://doi.org/10.1111/j.1469-8137.2008.02525.x)
- Ower R (1982) Notes on the development of the morel ascocarp: *Morchella esculenta*. *Mycologia* 74:142–144

- Palmer JG (1969) Techniques and procedures for culturing ectomycorrhizal fungi. In: Mycorrhizae: the first North American conference on mycorrhizae. USDA-Forest Service Miscellaneous Publication 1189. USDA, Washington, DC
- Parke JL, Linderman RG, Black CH (1983) The role of ectomycorrhizae in drought tolerance of Douglas-fir seedlings. *New Phytol* 95:83–95
- Peay KG, Bruns TD, Kennedy PG, Bergemann SE, Garbelotto M (2007) A strong species-area relationship for eukaryotic soil microbes: island size matters for ectomycorrhizal fungi. *Ecol Lett* 10:470–480. doi:[10.1111/j.1461-0248.2007.01035.x](https://doi.org/10.1111/j.1461-0248.2007.01035.x)
- Peay KG, Kennedy PG, Bruns TD (2011) Rethinking ectomycorrhizal succession: are root density and hyphal exploration types drivers of spatial and temporal zonation? *Fungal Ecol* 4:233–240. doi:[10.1016/j.funeco.2010.09.010](https://doi.org/10.1016/j.funeco.2010.09.010)
- Pena R, Offermann C, Simon J, Naumann PS, Geßler A, Holst J, Dannenmann M, Mayer H, Kögel-Knabner I, Rennenberg H, Polle A (2010) Girdling affects ectomycorrhizal fungal (EMF) diversity and reveals functional differences in EMF community composition in a Beech forest. *Appl Environ Microbiol* 76:1831–1841. doi:[10.1128/AEM.01703-09](https://doi.org/10.1128/AEM.01703-09)
- Perez-Moreno J, Martínez-Reyes M, Yescas-Pérez A, Delgado-Alvarado A, Xoconostle-Cázares B (2008) Wild mushroom markets in central Mexico and a case study at Ozumba. *Econ Bot* 62:425–436. doi:[10.1007/s12231-008-9043-6](https://doi.org/10.1007/s12231-008-9043-6)
- Pilz D, Molina R (1996) Managing forest ecosystems to conserve fungus diversity and sustain wild mushroom harvests. General Technical Report PNW-GTR-371. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR
- Pilz D, Norvell L, Dannel E, Molina R (2003) Ecology and management of commercially harvested chanterelle mushrooms. USDA General Technical Report. USDA, Portland, OR, pp 1–83. <http://www.fs.fed.us/pnw/pubs/gtr576.pdf>
- Raffle VL, Doudrick RL, Nelson CD, Furnier GR (1995) Genetic-analysis of homokaryons from a basidiome of *Laccaria bicolor* using random amplified polymorphic DNA (RAPD) markers. *Mycol Res* 99:1361–1366. doi:[10.1016/S0953-7562\(09\)81222-7](https://doi.org/10.1016/S0953-7562(09)81222-7)
- Rinaldi A, Comandini O, Kuyper T (2008) Ectomycorrhizal fungal diversity: separating the wheat from the chaff. *Fungal Divers* 33:1–45
- Rossi MJ, Furigo A, Oliveira VL (2007) Inoculant production of ectomycorrhizal fungi by solid and submerged fermentations. *Food Technol Biotechnol* 45:277–286
- Ruan-Soto F, Garibay-Orijel R, Cifuentes J (2006) Process and dynamics of traditional selling wild edible mushrooms in tropical Mexico. *J Ethnobiol Ethnomed* 2:3. doi:[10.1186/1746-4269-2-3](https://doi.org/10.1186/1746-4269-2-3)
- Schoch CL, Seifert KA, Huhndorf S, Robert V, Spouge JL, Levesque CA, Chen W, Bolchacova E, Voigt K, Crous PW, Miller AN, Wingfield MJ, Aime MC, An KD, Bai FY, Barreto RW, Begerow D, Bergeron MJ, Blackwell M, Boekhout T, Bogale M, Boonyuen N, Burgaz AR, Buyck B, Cai L, Cai Q, Cardinali G, Chaverri P, Coppins BJ, Crespo A, Cubas P, Cummings C, Damm U, de Beer ZW, de Hoog GS, Del-Prado R, Dieguez-Urbeondo J, Divakar PK, Douglas B, Duenas M, Duong TA, Eberhardt U, Edwards JE, Elshahed MS, Fliegerova K, Furtado M, Garcia MA, Ge ZW, Griffiths GW, Griffiths K, Groenewald JJ, Groenewald M, Grube M, Gryzenhout M, Guo LD, Hagen F, Hambleton S, Hamelin RC, Hansen K, Harrold P, Heller G, Herrera G, Hirayama K, Hirooka Y, Ho HM, Hoffmann K, Hofstetter V, Hognabba F, Hollingsworth PM, Hong SB, Hosaka K, Houbroken J, Hughes K, Huhtinen S, Hyde KD, James T, Johnson EM, Johnson JE, Johnston PR, Jones EB, Kelly LJ, Kirk PM, Knapp DG, Koljalg U, Kurtzman CP, Landvik S, Leavitt SD, Liggenstoffer AS, Liimatainen K, Lombard L, Luangsa-Ard JJ, Lumsch HT, Maganti H, Maharachchikumbura SS, Martin MP, May TW, McTaggart AR, Methven AS, Meyer W, Moncalvo JM, Mongkolsamrit S, Nagy LG, Nilsson RH, Niskanen T, Nyilasi I, Okada G, Okane I, Olariaga I, Otte J, Papp T, Park D, Petkovits T, Pino-Bodas R, Quaedvlieg W, Raja HA, Redecker D, Ruibal C, Sarmiento-Ramirez JM, Schmitt I, Schussler A, Shearer C, Sotome K, Stefani FO, Stenroos S, Stielow B, Stockinger H, Suetrong S, Suh SO, Sung GH, Suzuki M, Tanaka K, Tedersoo L, Telleria MT, Tretter E, Untereiner WA, Urbina H, Vagvolgyi C, Vialle A, Vu TD, Walther G, Wang QM, Wang Y, Weir BS, Weiss M,

- White MM, Xu J, Yahr R, Yang ZL, Yurkov A, Zamora JC, Zhang N, Zhuang WY, Schindel D, Consortium FB (2012) Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for fungi. *Proc Natl Acad Sci USA* 109:6241–6246. doi:[10.1073/pnas.1117018109](https://doi.org/10.1073/pnas.1117018109)
- Seifert KA (2009) Progress towards DNA barcoding of fungi. *Mol Ecol Resour* 9:83–89. doi:[10.1111/j.1755-0998.2009.02635.x](https://doi.org/10.1111/j.1755-0998.2009.02635.x)
- Sha T, Xu J, Palanichamy MG, Zhang H-B, Li T, Zhao Z-W, Zhang Y-P (2008) Genetic diversity of the endemic gourmet mushroom *Thelephora ganbajun* from southwestern China. *Microbiology* 154:3460–3468. doi:[10.1099/mic.0.2008/020495-0](https://doi.org/10.1099/mic.0.2008/020495-0)
- Smith ME, Pfister DH (2009) Tuberculate ectomycorrhizae of angiosperms: the interaction between *Boletus rubropunctus* (Boletaceae) and *Quercus* species (Fagaceae) in the United States and Mexico. *Am J Bot* 96:1665–1675. doi:[10.3732/ajb.0900058](https://doi.org/10.3732/ajb.0900058)
- Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, London
- Smith ME, Douhan GW, Rizzo DM (2007a) Ectomycorrhizal community structure in a xeric quercus woodland based on rDNA sequence analysis of sporocarps and pooled roots. *New Phytol* 174:847–863. doi:[10.1111/j.1469-8137.2007.02040.x](https://doi.org/10.1111/j.1469-8137.2007.02040.x)
- Smith ME, Douhan GW, Rizzo DM (2007b) Intra-specific and intra-sporocarp its variation of ectomycorrhizal fungi as assessed by rDNA sequencing of sporocarps and pooled ectomycorrhizal roots from a quercus woodland. *Mycorrhiza* 18:15–22. doi:[10.1007/s00572-007-0148-z](https://doi.org/10.1007/s00572-007-0148-z)
- Taylor JW, Berbee ML (2006) Dating divergences in the fungal tree of life: review and new analyses. *Mycologia* 98:838–849. doi:[10.3852/mycologia.98.6.838](https://doi.org/10.3852/mycologia.98.6.838)
- Tedersoo L, May TW, Smith ME (2010) Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* 20:217–263. doi:[10.1007/s00572-009-0274-x](https://doi.org/10.1007/s00572-009-0274-x)
- Trappe JM, Strand RF (1969) Mycorrhizal deficiency in a Douglas-fir region nursery. *For Sci* 15:381–389
- Trappe MJ, Evans F, Trappe JM (2007) Field guide to North American truffles. Ten Speed, Berkeley, CA, 136p
- Trappe J, Claridge A, Claridge D, Liddle L (2008) Desert truffles of the Australian outback: ecology, ethnomycology, and taxonomy. *Econ Bot* 62:497–506. doi:[10.1007/s12231-008-9041-8](https://doi.org/10.1007/s12231-008-9041-8)
- Trappe J, Molina R, Luoma D, Cazares E, Pilz D, Smith JE, Castellano M, Miller S, Trappe M (2009) Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest. PNW-GTR-772. FS United States Department of Agriculture, Pacific Northwest Research Station, Portland, OR, 194p
- Trappe MJ, Trappe JM, Bonito GM (2010) *Kalapuya brunnea* gen. & sp. nov. and its relationship to the other sequestrate genera in *Morchellaceae*. *Mycologia* 102:1058–1065. doi:[10.3852/09-232](https://doi.org/10.3852/09-232)
- Urban A, Neuner-Plattner I, Krisai-Greilhuber I, Haselwandter K (2004) Molecular studies on terricolous microfungi reveal novel anamorphs of two *Tuber* species. *Micol Res* 108:749–758
- van Dijk H, Onguene NA, Kuyper TW (2003) Knowledge and utilization of edible mushrooms by local populations of the rain forest of south Cameroon. *Ambio* 32:19–23
- Varda Kagan-Zur V, Roth-Bejerano N (2008) Unresolved problems in the life cycle of truffles. *Open Mycol J* 2:86–88
- Visnovsky SB, Guerin-Laguette A, Wang Y, Pitman AR (2010) Traceability of marketable Japanese shoro in New Zealand: using multiplex PCR to exploit phylogeographic variation among taxa in the *Rhizopogon* subgenus *Roseoli*. *Appl Environ Microbiol* 76:294–302. doi:[10.1128/AEM.02191-09](https://doi.org/10.1128/AEM.02191-09)
- Wang Y, Hall IR (2004) Edible ectomycorrhizal mushrooms: challenges and achievements. *Can J Bot* 82:1063–1073
- Winder RS (2006) Cultural studies of *Morchella elata*. *Micol Res* 110:612–623. doi:[10.1016/j.mycres.2006.02.003](https://doi.org/10.1016/j.mycres.2006.02.003)

- Yamada A, Ogura T, Ohmasa M (2001) Cultivation of mushrooms of edible ectomycorrhizal fungi associated with *Pinus densiflora* by in vitro mycorrhizal synthesis I. Primordium and basidiocarp formation in open-pot culture. *Mycorrhiza* 11:59–66
- Yun W, Hall IR, Evans LA (1997) Ectomycorrhizal fungi with edible fruiting bodies: *Tricholoma matsutake* and related fungi. *Econ Bot* 51:311–327

Edible Ectomycorrhizal Mushrooms  
Current Knowledge and Future Prospects  
Zambonelli, A.; Bonito, G.M. (Eds.)  
2012, XII, 409 p., Hardcover  
ISBN: 978-3-642-33822-9