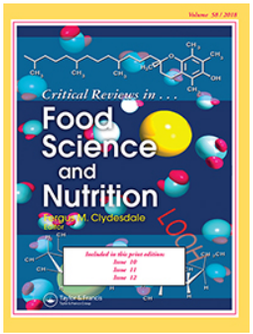

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True morels (*Morchella*)—nutritional and phytochemical composition, health benefits and flavor: A review

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ABSTRACT

Morels are edible mushrooms appreciated worldwide for their savory flavor. Morels have been in use in traditional medicine for centuries, due to their health-related benefits, and current research demonstrated their anti-oxidative and anti-inflammatory bioactivities, in addition to immunostimulatory and anti-tumor properties. In spite of the high demand for morels and their increasing economic importance, their cultivation is limited, and they are either used as wild harvested or fermented in culture, for consumption as a functional food and for food-flavoring. Morel's health benefits were attributed mainly to polysaccharides as the active compounds, and to various phytochemicals, mainly phenolic compounds, tocopherols, ascorbic acid and vitamin D. Morel's nutritional composition was reported, including sugar, amino acid, fatty and organic acid and mineral profile. Information regarding Morel's flavor is limited, and while some of their taste attributes have been described, including the role of umami taste, details about their volatile aroma profile are scarce, and it was reported to include eight carbon volatiles, the main aroma volatiles typical to most mushrooms. To the best of our knowledge, this is the first review presenting morels' nutritional and phytochemical composition, health benefits and flavor, and we will review the available information in current literature regarding these aspects in light of morels phenotypic plasticity.

KEYWORDS

Aroma; health; flavor; morchella; morel; nutritional composition; phytochemicals; taste

Introduction

Morels (*Morchella spp*, Pezizales, Ascomycota) are edible mushrooms, highly appreciated among gastronomists for their desirable taste quality, and culinary prized in many cuisines for their rich unique aroma, delicate flavor and meaty texture (Phillips and Phillips, 1991). Morels are consumed worldwide as food, and in Tibet and India are cooked with vegetables and considered as notorious as meat or fish (Ajmal et al., 2015). Thanks to their noticeable umami taste, morels are also consumed as food-flavoring agent (Litchfield, 1967, Mau et al., 2004), used fresh or after air or freeze-drying. Commercial cultivation of morels is currently very limited, and only three cases of its domestication were reported, in Israel, USA, and China (Ower, 1982, Zhao et al., 2009, Masaphy, 2010). Morels are thus harvested in the wild (Winder, 2006), mainly in China, India, Turkey, Mexico, and USA (Pilz, 2008), where they are abundant in wild growth. For food-flavoring purposes, morels are also fermented *in-vitro* as a mycelia in a submerged culture (Litchfteld et al., 1963), and these cultures have been characterized and optimized (Mau et al., 2004, Tsai et al., 2006, Winder, 2006). Due to the increasing demand, currently standing at 900,000 kg annually averaging at $160 USD per kilogram (Du et al., 2015), morchella is becoming of high economic importance (Sher et al., 2014, Ajmal et al., 2015). This is especially prominent in areas where morels are harvested by locals (Prasad et al., 2002), to be further commercially marketed or exported (Ali et al., 2011, Mahmood et al., 2011, Sher et al., 2015).

Morels are characterized by a unique conic head, with a honeycomb appearance, resulting from a network of ridges with pits composing their cap. Their various habitats include roads and road cuts, excavation, lightly burned grassy areas and swampy ground, and they were mostly reported in areas destroyed by fire (Prasad et al., 2002, Negi, 2006, Huffman, 2008). *Morchella* sp. fruiting bodies (morels) are highly polymorphic in shape, immature and mature color, taste and edibility (Weber, 1997, Kuo, 2005, Masaphy et al., 2010), and the range of species within *Morchella* genus differ in color, chemical composition and bioactivity. Morel collectors distinguish between black morels, such as *Morchella conica, M. angusticeps, M. elata, M. vulgaris*, and yellow morels, which include *M. esculenta, M. crassipes*, and *M. deliciosa* (Weber, 1997, Kuo, 2005). The yellow morel *M. esculenta* and the black morel *M. conica* are the most studied species in regard to nutritional and phytochemical composition, due to their high consumption. However, recent studies of molecular speciation of morels using multigene molecular phylogenetic assessment approach (Richard et al., 2015) revealed that the phenotypic identification of morels is questionable, as species diversity is much higher when using molecular identification techniques, is compared to former phenotypic-based systematics.

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In light of morel high diversity and plasticity, and the challenge of having a whole picture on morel bioactivity characteristics, we have reviewed here the current literature regarding morel's nutritional composition and phytochemical contents. This is in addition to the evidences of suggested health benefits in consumption of the different reported *Morchella* species, either using the whole morel mushroom or its mycelial biomass. The aspects of their taste and aroma are also reviewed in perspective of other edible mushrooms investigated. Health-promoting effects and bioactivities reports of various *Morchella* species are summarized in Table 1.

Health-related effects of mushrooms

Mushrooms were in use for centuries in traditional medicine (Wasser and Weis, 1999), and played an important role in both Chinese Traditional Medicine (TCM) and western pharmacopeia (Lindequist et al., 2005, Sullivan et al., 2006). Current scientific research has profiled some of their bioactive constituents and properties, as well as confirmed some of their medicinal features (Gao, 2006, Barros et al., 2008, Zhong and Xiao, 2009, Greve et al., 2010, Stajic et al., 2013, Beekman and Barrow, 2014, Evidente et al., 2014, Giavasis, 2014, Huang and Nie, 2015, Zhang, 2015, Chatterjee and Acharya, 2016, Zhang et al., 2016). Mushrooms' significant antibacterial, antioxidant and anti-inflammatory as well as immunomodulation, antitumor and anti-inflammatory features were described (Ooi and Liu, 2000, Wasser, 2002, Ferreira et al., 2009, Roupas et al., 2012, Stajic et al., 2013, Evidente et al., 2014, Taofiq et al., 2016), in addition to protective effects on beta-amyloid peptide toxicity (as a precursor of dementia) (Roupas et al., 2012). Furthermore, their anti-viral, anti-microbial, anti-fungal, anti-allergic, anti-atherogenic and hypoglycemic activities were also reported (Lindequist et al., 2005, Alves et al., 2012, Roupas et al., 2012), as well as their anti-diabetic, cardiovascular, and hepatoprotective effects (Wasser and Weis, 1999, Guillamón et al., 2010, Wasser, 2010, Roupas et al., 2012, Chatterjee and Acharya, 2016).

Mushrooms' medicinal bioactivity is attributed primarily to polysaccharides as the biologically active component (Huang and Nie, 2015), either in the form of β-D-glucans or as polysaccharide–protein complexes (Lindequist et al., 2005, Zhang et al., 2007). It was suggested that mushrooms exert their immunoregulatory effects and other health benefits via balance of T helper cells, and induction of certain interleukins and interferon-gamma or NO-mediated mechanisms (Roupas et al., 2012). Other health-related phytochemicals in mushrooms also regarded as responsible for health benefits include phenolic compounds, tocopherols, ascorbic acid and carotenoids, whose effects are mainly attributed to their high antioxidative activity (Ferreira et al., 2009, Kalač, 2009, Leal et al., 2013). Due to their health-promoting properties, mushrooms have recently become attractive also as functional foods (Chang, 2008, Cheung, 2008).

Health-related effects of morels

Morchella use in traditional medicine was reported for wounds, for rapid healing and as antiseptic (Mahmood et al., 2011), for digestive system symptoms (Mahmood et al., 2011, Lone et al., 2012), as an immunostimulant (Prasad et al., 2002), as a general tonic (Rokaya et al., 2010, Ali et al., 2011, Sher et al., 2014) and for cold and coughs (Nautiyal et al., 2001), and in TCM it was prescribed for indigestion, excessive phlegm, and shortness of breath (Jianzhe and Xiaolan, 1987, Duncan et al., 2002).

Morels are currently in use as a nutraceutical and as a functional food (Mau et al., 2004, Tsai et al., 2006), and a few studies examined their bioactivities. Nitha and co-workers reported the nephroprotective effect of aqueous-ethanolic extract of *M. esculenta* mycelia against cisplatin and gentamicin-induced nephrotoxicity in mice (Nitha and Janardhanan, 2008). Later on, the same authors reported the anti-hepatotoxic and hepatoprotective activity of aqueous-ethanolic extract of cultured mycelia of *M. esculenta* against CCl_4 and ethanol-induced chronic hepatotoxicity (Nitha et al., 2013). Moreover, anti-inflammatory activity of morels was reported, showing significant dose-dependent inhibition of both acute and chronic inflammation (Nitha et al., 2007), as well as a decrease in intracellular oxidation status in HT-29 colon cancer cells, and significant inhibition of the pro-inflammatory cytokine NF-κB activation (Kim et al., 2011). Anti-tumor activity of the ethanolic extract of cultured mycelia of *M. esculenta* was determined using both Dalton's lymphoma ascites (DLA) cell line-induced solid tumor and Ehrlich's ascites carcinoma (EAC) cell line-induced tumor models in mice, and exhibited significant anti-tumor activity against both ascites and solid tumors (Nitha et al., 2007). The authors thus suggested the potential therapeutic use of aqueous-ethanolic extract of morel mushroom mycelia in chemotherapy (Nitha et al., 2007). Evaluation of anti-mutagenic and anti-mitotic effects of *M. esculenta* found that methanolic extracts expressed important anti-mutagenic potency toward *S. typhimurium* (Stojkovic et al., 2013)

Polysaccharides

Many of Morel's health-promoting effects and bioactivities are ascribed to polysaccharides. Several works over the years described polysaccharides' properties, including their isolation and characterization of their structure and activities, for both endo and exo-polysaccharides. Specifically, endo-polysaccharide of *M. esculenta* submerged fermentation was reported to induce significant anti-hyperlipidemic and anti-atherosclerosis activities; anti-hyperlipidemic potential was determined by detecting body weights and serum lipid index of hyperlipidemic mice. The endo-polysaccharide caused a decrease in body weight in a dose-dependent manner, and a non-dose-dependent alteration in serum lipid index (Liu et al., 2016). Induction of apoptosis in HepG2 cells by the polysaccharide *M.esculenta* polysaccharide (MEP)-II from the fermentation broth of *M. esculenta* was also reported (Hu et al., 2013), in addition to *in vivo* investigation of the effects of its mycelia extract on the ethanol-induced gastric mucosal lesions of rats, showing protective effects of the extract against the ethanol-induced gastric lesions, possibly due to increased superoxide dismutase (SOD) activity and decreased malondialdehyde (MDA) level in rats (Wei et al., 2011). Anti-proliferating and anti-tumor activities of a *M. esculenta* polysaccharide extracted by pulsed electric field (PEF) in submerged fermentation were evaluated, and

Table 1. Health-promoting effects and bioactivities of various Morchella species.

Species	Method	Extract	Origin	Activity	Reference
			Mushrooms		
M. esculenta	Inhibition of NF-κB activation	methylene chlorid	US	Anti-inflammatory	Kim et al., 2011
M. esculenta	Increasing NF-κB expression	galacto-mannan	US	Immunostimulatory	Duncan et al., 2002
M. esculenta	*S. typhimurium* bioassay	methanol	Portugal and Serbia	Anti-mutagenic and anti-mitotic	Stojkovic et al., 2013
M. vulgaris, M. esculenta	Reducing power ability	ethanol	Turkey	*M. vulgaris*>*M. esculenta*	Elmastas et al., 2006
Morchella spp.	Reducing power ability	methanol	Turkey	0.062–0.145 at 0.5mg/ml, 0.563–1.055 at 4.5 mg/ml	Gursoy et al., 2009
M. conica	Reducing power ability	methanol	Portugal and Serbia	EC50=1.16 and 1.88 mg/ml, respectively	Vieira et al., 2016
M. esculenta	Reducing power ability	methanol	Portugal and Serbia	EC50=6.34 and 1.26 mg/ml, respectively	Heleno et al., 2013
M. conica	Reducing power ability	water and methanol	India	3.9 and 8.6 GAE/g DW, respectively	Puttaraju et al., 2006
M. anguisticeps	Reducing power ability	water and methanol	India	7.56 and 2.42 mg GAE/g DW, respectively	Puttaraju et al., 2006
M. esculenta vs. M. vulgaris	Radical scavenging activity	methanol	Israel	*M. vulgaris*>*M. esculenta*	Jander-Shagug and Masaphy, 2010
M. vulgaris, M. esculenta	Scavenging effects	ethanol	Turkey	95% and 94%, at 180 μg/mL, respectively	Elmastas et al., 2006
Morchella spp.	Radical scavenging activity	methanol	Turkey	3.96%-13.91% for *M. deliciosa* at 0.5 mg/ml to 40.63%-85.36% for M. conica at 4.5 mg/ml	Gursoy et al., 2009
Morchella spp.	Scavenging effects	methanol	Turkey	43.97%-52.44% at 8 μg/ml to 58.47%-78.66% at 40 μg/ml	Gursoy et al., 2009
M. conica	Anti-radical activity	methanol	Turkey	43.8% at 20 mg/ml	Ozturk et al., 2010
M. conica	Anti-radical activity	ethanol	Turkey	IC50=267 μg/ml	Turkoglu et al., 2006
M. vulgaris, M. esculenta	Scavenging effects	ethanol	Turkey	95% and 94%, at 180 μg/mL, respectively	Elmastas et al., 2006
M. conica	Scavenging activity	methanol	Portugal and Serbia	EC_{50}= 3.56 and 9 mg/ml, respectively	Vieira et al., 2016
M. esculenta	Scavenging activity	methanol	Portugal and Serbia	EC_{50}= 6.06 and 3.03 mg/ml, respectively	Heleno et al., 2013
M. conica	Radical scavenging activity	water and methanol	India	0.3 and, 0.94 mg BHA equivalent/g DW, respectively IC_{50}= 5 and 1.6 mg/ml, respectively	Puttaraju et al., 2006
M. anguisticeps	Radical scavenging activity	water and methanol	India	0.88 and 0.73 mg BHA/g, respectively, IC_{50} = 1.65 and 2.09 mg/ml, respectively	Puttaraju et al., 2006
M. esculenta	Scavenging effects	Water	Spain	45% scavenging	Ramírez−Anguiano et al., 2007
M. esculenta	Radical scavenging activity	methanol	Spain	more than 90% at 1.8 mg/ml	Ramírez−Anguiano et al., 2007
M. vulgaris, M. esculenta	Inhibition of superoxide generation	ethanol	Turkey	84% and 83% at 100 μg/ml, respectively	Elmastas et al., 2006
M. conica	Lipid peroxidation inhibition	ethanol	Turkey	77.9% inhibition at 80 μg/ml, 96.9% inhibition at 160 μg/ml	Turkoglu et al., 2006
Morchella spp.	Lipid peroxidation capacity	methanol	Turkey	63.18%–86.77% at 0.5 mg/ml, 94.37%–96.89% at 4.5 mg/ml	Gursoy et al., 2009
M. esculenta	Lipid peroxidation inhibition	methanol	Portugal and serbia	EC_{50}=0.81 and 2.39 mg/ml, respectively	Heleno et al., 2013
M. conica	Lipid peroxidation inhibition	methanol	Portugal and Serbia	EC_{50}=2.5 and 0.8 mg/ml, respectively	Vieira et al., 2016
M. esculenta	Lipid peroxidation inhibition (TBARS)	methanol	Portugal and Serbia	EC_{50}=1.01 and 2.23 mg/ml, respectively	Heleno et al., 2013
M. conica	Lipid peroxidation inhibition	methanol	Portugal and Serbia	EC_{50}=0.55 and 0.3 mg/ml, respectively	Vieira et al., 2016
M. conica	Lipid peroxidation inhibition	water and methanol	India	65 and 277 nmol MDA/mg phenolics, respectively	Puttaraju et al., 2006
M. anguisticeps	Lipid peroxidation inhibition	water and methanol	India	57.5 and 374.0 nmol of MDA/mg of phenolics	Puttaraju et al., 2006
Morchella spp.	Chelating effects on ferrous ions	methanol	Turkey	82.33%-89.9% at 0.05 mg/ml to 88.08%-96.68% at 0.25 mg/ml	Gursoy et al., 2009

			Mycelium and fermentation broth		
M. esculenta	Induced nephrotoxicity *in-vivo*	aqueous-ethanol	mycelium	Nephroprotective	Nitha and Janardhanan, 2008
M. esculenta	Induced chronic hepatotoxicity *in-vivo*	aqueous-ethanol	mycelium	Anti-hepatotoxic, hepatoprotective	Nitha et al., 2013
M. esculenta	Inhibition of acute and chronic inflammation *in-vivo*	ethanol	mycelium	Anti-inflammatory	Nitha et al., 2007
M. esculenta	Induced lymphoma and carcinoma *in-vivo*	ethanol	mycelium	Anti-tumor	Nitha et al., 2007
M. esculenta	Serum lipid index and body weight *in-vivo*	endo-PS	submerged fermentation	Anti-hyperlipidemic, anti-atherosclerosis	Liu et al., 2016
M. esculenta	HepG2 cells apoptosis	PS-MEP-II	fermentation broth	Induction of apoptosis	Hu et al., 2013
M. conica.	Induced gastric mucosal lesions *in-vivo*	PS	mycelium	Protective effects against gastric lesions Increased SOD activity, decreased MDA level	Wei et al., 2011
M. esculenta	Apoptosis in human colon cancer HT-29 cells	PEF extracted PS	submerged fermentation	Anti-proliferating and anti-tumor	Liu et al., 2016
M. esculenta	*In-vivo* SOD and GSH-Px activity	SO-01 exo-PS	submerged mycelial culture	Anti-oxidant Reducing lipid peroxidation	Meng et al., 2010
M. esculenta	*In-vivo* anti-oxidative and reducing capacity	SO-02 exo-PS	submerged mycelial culture	Anti-oxidative, SOD EC_{50} = 105 mg/l, Hydroxyl radical EC_{50} = 103 mg/l, increased reducing capacity of 0.48 (abs.) at 200 mg/l	Meng et al., 2010
M. conica	Nitric oxide production modulation in macrophages	mannan exo-PS	submerged mycelial culture	Immunomodulatory	Su et al., 2013
M. esculenta	*In-vivo* Immunomodulatory and immunostimulatory activities	MEP I and II PS	China	Immunomodulatory and immunostimulatory activities	Cui et al., 2011
M. esculenta	Reducing power ability	methanol	mycelium	0.11 (Abs.) at 0.5 mg/ml and 0.97 at 25 mg/ml, EC_{50}=1.25 mg/ml	Mau et al., 2004
M. esculenta	Scavenging effect	methanol	mycelium	94.1% at 10 mg/ml, EC_{50}= 3.71 mg/ml	Mau et al., 2004
M. esculenta	Radical scavenging activity	ethanol	mycelium	0.1%, 0.5%, and 1% scavenged 20.46%, 30.96%, and 53.79%, respectively	Nitha et al., 2010
M. esculenta	Radical scavenging capacity	aqueous-ethanol	mycelium	IC_{50}=87.5 μg/ml	Nitha et al., 2010
M. esculenta	Scavenging of hydroxyl radicals	aqueous-ethanol	mycelium	IC_{50}=363.33 μg/ml	Nitha et al., 2010
M. esculenta	Scavenging of hydroxyl radicals	methanol	mycelium	0%–2.1% at 0.5–10 mg/ml	Mau et al., 2004
M. esculenta	Antioxidant activities	methanol	mycelium	85.4– 94.7% at 25 mg/ml, EC_{50}=2.78 mg/ml	Mau et al., 2004
M. esculenta	Inhibition of superoxide generation	aqueous-ethanol	mycelium	IC_{50}=244 μg/ml	Nitha et al., 2010
M. esculenta	lipid peroxidation inhibition	aqueous-ethanol	mycelium	IC_{50}=420 μg/ml	Nitha et al., 2010
M. esculenta	Chelating effects on ferrous ions	methanol	mycelium	Low at 0.5–1.0 mg/ml, high at 5–25 mg/ml $EC_{50=}$3.55 mg/ml	Mau et al., 2004

SOD- superoxide dismutase; MDA- malondialdehyde; PEF- pulsed electric field; GSH-Px - glutathione peroxidase; GAE- gallic acid equivalent ; PS- polysaccharides; TBARS- thiobarbituric acid reactive species.

apoptosis tests proved that they could inhibit the proliferation and growth of human colon cancer HT-29 cells in a time-and dose-dependent manner within 48 hours (Liu et al., 2016).

A high-molecular-weight galactomannan, about 1.0 million Da, comprised of mannose (62.9%) and galactose (20.0%), was described by Duncan et al period, which at 3.0 μg/mL exhibited immunostimulatory activity of increasing NF-κB expression (Duncan et al., 2002). Liu et al described the anti-proliferating and antitumor activity of *M. esculenta* endo-polysaccharide from a submerged fermentation, with a molecular weight of 81,835 Da, which consisted of xylose, glucose, mannose, rhamnose and, galactose at the ratio of 5.4:5.0:6.5:7.8:72.3 (Liu et al., 2016). Isolation, purification, and characterization of polysaccharides from fruit body of *M. esculenta* were recently described by Yang and co-workers (Yang et al., 2015). These polysaccharides were primarily polymers of glucose, mannose, galactose and arabinose, with an average molecular mass of 43,625 Da (Yang et al., 2015). Two other polysaccharides from *M. esculenta* (MEP I and II) were purified and characterized by Cui et al., with average molecular weights of 192 and 53.3 kDa, showing immunomodulatory and immunostimulatory activities (Cui et al., 2011). MEP I was a heteropolysaccharide consisting of arabinose, mannose, glucose and galactose, with the molar ratio of 0.7: 2.8: 24.8: 1.0. MEP-II was also a heteropolysaccharide, consisting of rhamnose, mannose, glucose and galactose, with the molar ratio of 1.8: 3.1: 21.4: 1.0. The glucose contents in MEP-I and MEP-II were 84.64% and 78.39%, respectively.

Several other papers studied different parameters of fermentation, aiming at optimizing the production process. Xu et al. reported the optimized cultivation conditions, by investigating the effects of fermentation time, temperature and broth content on mycelial growth (dry cell weight) and extracellular polysaccharide content produced by *M. esculenta* As51620 in submerged fermentation (Xu et al., 2008). Li et al. suggested using soybean curd residue for *M. esculenta* fermentation, at optimized conditions (Li et al., 2013). In two works, Meng et al. reported the optimization of production and extraction of exopolysaccharides SO-01 and SO-02 from submerged cultures of *M. esculenta*, as well as their anti-oxidative activities (Meng et al., 2010). Evaluation of *in vivo* antioxidant activity showed that SO-01 can increase antioxidant abilities by improving superoxide dismutase and glutathione peroxidase (GSH-Px) activities, and reducing lipid peroxidation in blood, liver, heart, spleen and kidney of mice (Meng et al., 2010). *In vitro* anti-oxidative activity of SO-02 was also evaluated, showing an EC_{50} value of superoxide radical scavenging activity of 105 mg/L, EC_{50} value for hydroxyl radical scavenging activity of 103 mg/L, and remarkable reducing capacity of 0.48 (absorbance units) at a dose of 200 mg/L (Meng et al., 2010). Su and co-workers reported the Isolation and characterization of homogeneous mannan exopolysaccharide from submerged mycelial culture of *M. conica*, with an average molecular weight of approximately 81.2 kDa (Su et al., 2013). These authors also characterized its immunomodulatory activity, showing it was able to significantly modulate nitric oxide production in macrophages, and promote splenocytes proliferation (Su et al., 2013). All these results provide a reference for large-scale extraction of polysaccharides of morchella species, and reflect the high interest in using industrial conditions for *Morchella* polysaccharide fermentation, to be used as functional foods.

Antioxidants

Anti-oxidative properties in mushrooms were correlated to different antioxidative components such as tocopherols, carotenoids, ascorbic acid and total phenolics (Barros et al., 2007, Barros et al., 2008, Jander-Shagug and Masaphy, 2010), although different phenolic compounds seem to be the most effective group of antioxidants, while the role of tocopherols seems to be limited and that of β-carotene and lycopene vestigial (Barros et al., 2008, Kalač, 2009).

Specifically, *Morchella* anti-oxidative activities were thoroughly investigated, since nutritional anti-oxidants are of special interest as some scientific evidences exist showing that anti-oxidative activity is responsible for many of the health-promoting properties of foods and nutraceuticals (Shahidi and Ambigaipalan, 2015). Antioxidants were suggested to play a beneficial role by helping cellular defense systems (enzymes and non-enzymatic) cope with oxidative stress (Kurutas, 2016). Such oxidative stress is the result of normal cellular metabolism, and involves the formation of free radicals in the form of reactive oxygen and nitrogen species (ROS and RNS, respectively) (Apak et al., 2016). Oxidative stress and excessive free radical formation has also been related to a large number of chronic diseases, including cancer, diabetes, cardiovascular and neurological diseases, as well as to aging (Ferreira et al., 2009). Being unstable, these free radicals further react with DNA, protein and lipid membrane molecules causing cellular damage, hence involved in the onset of pathogenesis (Siti et al., 2015, Walton, 2016).

Nutritional anti-oxidants impose their positive effects by scavenging ROS and RNS, thus stabilizing oxidation processes and lowering the damage to cellular structures (Conti et al., 2016, Croft, 2016). The ingestion of substances with antioxidant activity was reported to be important in the prevention of oxidative stress and consequently in the prevention of health disorders (Pisoschi and Pop, 2015, Ataie et al., 2016). Natural antioxidants from plant origin are considered useful as nutraceuticals due to their beneficial effects on health and chronic disease prevention (Croft, 2016).

These nutritional anti-oxidants include both water-soluble compounds, e.g., polyphenols of various structural groups, polysaccharides, betalains, sulfides and thiols, glucosinolates and ascorbic acid, as well as lipid-soluble compounds, e.g., carotenoids, tocopherols and phytosterols.

Various methods exist to evaluate anti-oxidative capacity, which measure some of the aspects and mechanisms of anti-oxidative bioactivity. These multimechanistic antioxidative assays include, among others, determination of reducing power, inhibition of lipid peroxidation, free radical scavenging ability, chelating effects on ferrous ions and anti-oxidative enzymatic activity. Some of these assays were previously reviewed by Ferreira et al. in regard to antioxidants in wild mushrooms (Ferreira et al., 2009).

Reducing power ability. Reducing power ability is usually evaluated using the Ferricyanide/Prussian blue assay method. An EC_{50} value (mg/mL) is the effective concentration at which

the absorbance was 0.5 for reducing power and is obtained by interpolation from linear regression analysis. The reducing power activity of *M. conica* was reported to vary from 3.9 mg gallic acid equivalent (GAE)/g dry weight (DW) in water extracts to 8.6 mg GAE/g in methanol extracts, while that of *M. anguisticeps* varied from 7.56 to 2.42 mg GAE/g in water and methanol extracts, respectively (Puttaraju et al., 2006). The reducing power of the methanolic extract from *M. esculenta* mycelia was 0.11 (absorption units) at 0.5 mg/mL and 0.97 at 25 mg/mL, with EC_{50} value of 1.25 mg/mL (Mau et al., 2004). In a different study, Elmasta et al. reported that ethanol extracts of *M. vulgaris* from Turkey had higher reducing power compared to *M. esculenta*, but lower than control antioxidants (butylated hydroxytoluene (BHT) and butylated hydroxyanisole (BHA)). The authors, however, did not provide specific EC_{50} values (Elmastas et al., 2006). Recently, Vieira et al. reported that the reducing power of methanolic extracts of *M. conica* was significantly higher in samples from Serbia compared to those from Portugal, with EC_{50} values of 1.88 and 1.16 (absorption units), respectively (Vieira et al., 2016). Interestingly, the EC_{50} of methanolic extracts of *M. esculenta* from Portugal was 6.34 mg/mL, significantly higher than that of Serbian samples, with 1.26 mg/mL (Heleno et al., 2013). Gursoy et al. (Gursoy et al., 2009) studied the reducing power of *Morchella* species, which varied from 0.062 to 0.145 mg/mL at 0.5 mg/mL, to 0.563–1.055 at 4.5 mg/mL (Gursoy et al., 2009).

Free radical scavenging activity. Scavenging of free radical has been shown to inhibit the deleterious effects of oxidation in live cells. DPPH, a stable free radical, is used to study the radical scavenging effects of extracts, by measuring the scavenging activity. As antioxidants donate protons to these radicals, their absorption decreases, and this decrease is taken as a measure of the extent of radical scavenging. Inhibitory concentration to inhibit 50% of free radical scavenging activity is defined as IC_{50} value. The free radical scavenging activity of *M. conica* was reported to vary from 0.3 mg BHA equivalent/g DW in water extracts to 0.94 mg BHA/g in methanol extracts, with an IC_{50} value of 5 mg/mL and 1.6 mg/mL, respectively (Puttaraju et al., 2006). Free radical scavenging of *M. anguisticeps* varied from 0.88 mg BHA/g to 0.73 mg BHA/g in water and methanol extracts, respectively (Puttaraju et al., 2006), with an IC_{50} value of 1.65 mg/mL and 2.09 mg/mL, respectively (Puttaraju et al., 2006). In another study, the anti-radical activity of *M. conica* was determined using 20 mg/mL concentration of methanolic extracts, to be 43.8% (Ozturk et al., 2010). Turkoglu et al. measured the anti-radical activity of ethanolic extracts of *M. conica*, showing an IC_{50} value of 267 μg/mL (Turkoglu et al., 2006). Scavenging effect of methanolic extracts of *M. esculenta* at 10 mg/mL was reported as 94.1%, with an EC_{50} value at 3.71 mg/mL (Mau et al., 2004). Recently, Vieira et al. reported that the scavenging activity of methanolic extracts of *M. conica* was significantly lower in samples from Portugal compared to Serbian samples, with EC_{50} values of 3.56 and 9 mg/mL, respectively (Vieira et al., 2016). Interestingly, the EC_{50} of methanolic extracts of *M. esculenta* from Portugal was reported to be 6.06 mg/mL, significantly higher than 3.03 mg/mL of Serbian samples (Heleno et al., 2013). The scavenging effects of ethanol extracts of *M. vulgaris* from Turkey was higher than that of *M. esculenta*, with 95% and 94%, respectively, at 180 μg/mL (Elmastas et al., 2006). Radical scavenging activity of *M. esculenta* mycelia ethanolic extracts was calculated, and concentrations of 0.1%, 0.5%, and 1% scavenged 20.46%, 30.96%, and 53.79% DPPH radicals, respectively (Nitha et al., 2010). In another study, *M. esculenta* extract was able to scavenge more than 90% of the radical at concentrations of 1.8 mg/mL (Ramírez−Anguiano et al., 2007). Gursoy et al. reported the scavenging effects of Morchella species at different concentrations, varying from 3.96% to 13.91% at 0.5 mg/mL for *M. deliciosa*, to 40.63%–85.36% at 4.5 mg/mL for *M. conica* (Gursoy et al., 2009).

Another method for free radical scavenging capacity evaluation uses 2,2′- azinobis (3-ethylbenzothiazolin-6-sulphonic acid) (ABTS) as the free radical. In this assay, the efficiency of the extract is measured in scavenging ABTS radicals generated by the reaction between ABTS and ammonium persulfate. The activity of aqueous-ethanol extracts of *M. esculenta* mycelia was found to be dose-dependent, with an IC_{50} value of 87.5 μg/mL (Nitha et al., 2010). Morchella species showed scavenging effects from 43.97% to 52.44% at 8 μg/mL, to 58.47%–78.66% at 40 μg/mL (Gursoy et al., 2009). *M. esculenta* extracts were able to scavenge 45% of ABTS radical (Ramírez−Anguiano et al., 2007).

A third method for measuring scavenging activity involves superoxide as the free radical, generated by the photo reduction of riboflavin or by phenazine methosulphate (PMS)-NADH, and detected by nitroblue tetrazolium (NBT) reduction. The percentage inhibition of superoxide anion generation is then calculated. The IC_{50} of aqueous-ethanol extract of *M. esculenta* mycelia measured using this method was reported to be 244 μg/mL (Nitha et al., 2010). The percent inhibition of superoxide generation by 100 μg/mL ethanol extracts of *M. vulgaris* and *M. esculenta* was 84% and 83%, respectively (Elmastas et al., 2006).

Scavenging of hydroxyl radical is another method to evaluate anti-oxidative activity, by measuring the degradation of deoxyribose to thiobarbituric acid reactive species (TBARS) by hydroxyl radicals, generated by Fe3+-ascorbate system. The IC_{50} value of *M. esculenta* mycelia extract required to scavenge the generated hydroxyl radical was 363.33 μg/mL (Nitha et al., 2010). Another study on the capacity of methanolic extracts from *M. esculenta* mycelia to scavenge hydroxyl radicals reported values of 0%–2.1% (Mau et al., 2004).

Lipid peroxidation inhibition. Lipid peroxidation within the cell generates lipid peroxides, which act on cellular components, causing structural and functional damage of biomolecules. Thus, lipid peroxidation inhibition is an important parameter of anti-oxidative activity and has also been suggested to play a role in the prevention of chronic diseases (Halliwell and Gutteridge, 2015). Lipid peroxidation inhibition can be measured by the β-carotene-linoleic acid assay. In this method, anti-oxidative capacity is determined by measuring the bleaching of β-carotene or the inhibition of volatile organic compounds and conjugated diene hydroperoxides arising from linoleic acid oxidation. At 80 μg/mL, *M. conica* ethanolic extracts showed 77.9% inhibition, whereas at 160 μg/mL 96.9% inhibition was recorded (Turkoglu et al., 2006). The methanolic extracts of *M. esculenta* mycelia showed high antioxidant activities of 85.4%–94.7% at 25 mg/mL (Mau et al., 2004), with EC_{50}

of 2.78 mg/mL. Using this assay, the antioxidative capacity of *M. esculenta* from Serbia was 2.39 mg/mL, significantly higher than samples from Portugal, with 0.81 mg/mL (Heleno et al., 2013). Vieira et al. reported that *M. conica* samples from Portugal had higher anti-oxidative capacity compared to Serbian samples, with EC_{50} of 2.5 mg/mL and 0.8 mg/mL, respectively (Vieira et al., 2016). Gursoy et al. reported the lipid peroxidation capacity of morchella species, varying from 63%–86.77% at 0.5 mg/mL, to 94.37%–96.89% to most species at 4.5 mg/mL (Gursoy et al., 2009).

Another method for the evaluation of lipid peroxidation inhibition is the TBARS method. In this system, TBARS react with Malondialdehyde (MDA), a product released during lipid peroxidation, which can also be measured in rodents' tissue homogenate (liver, kidney etc.). An inhibition in lipid peroxidation by the sample will show a decrease in MDA levels. Water and methanol extracts of *M. conica* were reported to show 65 nmol of MDA/mg of phenolics and 277 nmol of MDA/mg of phenolics, respectively, and *M. anguisticeps* extracts showed 57.5 nmol of MDA/mg of phenolics and 374.0 nmol MDA/mg of phenolics, respectively (Puttaraju et al., 2006). Heleno et al. reported an EC_{50} value of 1.01 mg/mL and 2.23 mg/mL for *M. esculenta* from Portugal and Serbia, respectively (Heleno et al., 2013). Vieira et al. reported EC_{50} value of 0.55 mg/mL, for *M. conica* from Portugal, significantly different from EC_{50} value of 0.3 mg/mL for Serbian samples (Vieira et al., 2016). Reported IC_{50} value of aqueous-ethanol extracts of *M. esculenta* mycelia was 420 μg/mL (Nitha et al., 2010).

Chelating effects on ferrous ions. The most effective pro-oxidants present in food systems are ferrous ions (Yamauchi et al., 1988), thus a high chelating effect is an important aspect of anti-oxidative capacity. In this assay, the percentage of inhibition of ferrozine–Fe^{2+} complex formation is determined. The chelating effects of methanolic extracts of *M. esculenta* mycelia on ferrous ions were low and insignificant at 0.5–1.0 mg/mL, but notably high at 5–25 mg/mL, with EC_{50} of 3.55 mg/mL (Mau et al., 2004). The chelating effects of various *Morchella* species were evaluated by Gursoy et al., showing chelating effects from 82.33%–89.9% at 0.05 mg/mL, to 88.08%–96.68% at 0.25 mg/mL (Gursoy et al., 2009).

Nutritional composition and phytochemicals

Nutritional composition

Mushrooms are nutritionally appreciated for their high levels of protein, fiber and minerals (Cheung, 2010, Kalač, 2013). The nutritional value of some morchella species, including *M. crassipes, M. esculenta, M. hortensis, M. conica and M. elata* was reported, with 7.5–11.52 g protein, 2.2–3.9 gr fat, 6.7–14.6 gr ash and 74.55–80.5 gr carbohydrates per 100 gr DW, with 10 gr dry matter and 355–386 kcal in 100 gr fresh weight (FW) (Litchfteld et al., 1963, Beluhan and Ranogajec, 2011, Heleno et al., 2013, Vieira et al., 2016). Although mushroom composition may vary as a result of growth areas, maturity stage, soil and environmental conditions (Heleno et al., 2013, Li et al., 2016, Vieira et al., 2016) and hence varies among reports, these values are generally comparable among reports (Litchfteld et al., 1963, Rotzoll et al., 2006, Tsai et al., 2006, Beluhan and Ranogajec, 2011, Heleno et al., 2013, Vieira et al., 2016). Furthermore, *Morchella* sugar profile comprises of 0.21–0.71 g fructose, 0.99–11.54 g mannitol, 1.09–5.34 g trehalose, 43.07 g mannose, 0.086 g arabitol and 1.7–9.54 g glucose per 100 g DW (Rotzoll et al., 2006, Tsai et al., 2006, Beluhan and Ranogajec, 2011, Heleno et al., 2013, Vieira et al., 2016). Amino acid profile was also recorded in several works, and includes high levels of glutamic acid and alanine, while levels of other amino acids vary among varieties, with reports showing high levels of leucine, proline, aspartic acid, arginine, glycine and threonine (Litchfteld et al., 1963, Rotzoll et al., 2006, Tsai et al., 2006, Beluhan and Ranogajec, 2011). Mineral contents of morels was reported in details (Dursun et al., 2006, Gursoy et al., 2009, Ozturk et al., 2010).

Of special importance is the fatty acid profile of mushrooms, as polyunsaturated fatty acids are the precursors of a wide range of short-chain volatiles in fungi (Vandamme, 2003). Fatty acid profile of morels consists of C18:2n6 as the main fatty acid (linoleic acid, 63%–72%) followed by C18:1n9 (oleic acid, 9.7%–21%), C16:0 (palmitic acid, 9.5%–11%) and C18:0 (stearic acid, 1.5%–2.6%) (Řezanka et al., 1999, Heleno et al., 2013, Vieira et al., 2016), and in one report C18:3n3 (linolenic acid) ranging between 0.2%–7.2% (Heleno et al., 2013).

Morels also contain several organic acids, including oxalic acid (32.73–190 mg/100 g DW), quinic acid (0–880 mg/100 g DW), malic acid (0–199.1 mg/100 g DW), citric acid (0–233.4 mg/100 g DW) fumaric acid (17.38–561 mg/100 g DW) and ascorbic acid (13 mg/100 g DW), with total organic acids ranging between 279 and 1560 mg/100 g DW (Mau et al., 2004, Heleno et al., 2013, Vieira et al., 2016).

Phytochemicals

Reported groups of phytochemicals in morels include polyphenols, steroids (mainly sterol derivatives), tocopherols and carotenoids, although the occurrence of carotenoids is limited in mushrooms compared to plants (Kalač, 2009, Kalač, 2013).

Tocopherols, a group of nutritional phytochemicals (Shahidi and Ambigaipalan, 2015), were reported in morels, including α-tocopherol (1.4–6.2 μg/100 g DW), β-tocopherol (20 μg/100 g DW), γ-tocopherol (12.4–20.3 μg/100 g DW) and δ-tocopherol (3.9–98.6 μg/100 g DW) (Mau et al., 2004, Heleno et al., 2013, Vieira et al., 2016).

Recently, new evidences on the roles of vitamin D in human health were published (Autier et al., 2014), followed by an updated daily reference intakes (Ross et al., 2011). Specific attention was paid to mushrooms as a significant dietary source of vitamin D_2, ergocalciferol (provitamin D) and of its provitamin, ergosterol (Cashman et al., 2014). Mushrooms contain relatively high levels of ergosterol, ranging between 3000–7000 mg/kg^{-1} DW (Mattila et al., 2002, Phillips et al., 2011), and 0.3–59 μg/100 g FW vitamin D_2 (Teichmann et al., 2007). Moreover, some health benefits of mushrooms were related to these sterols and their derivatives (Lindequist et al., 2005, Kim et al., 2011, Roupas et al., 2012), including ergosterol peroxide (Krzyczkowski et al., 2009), fungisterol, lanosterol, neoergosterol, brassicasterol and others (Pinho et al., 2008, Kalač, 2009, Abd Malek et al., 2012, Phillips et al., 2012). Morel sterol

composition was not thoroughly investigated, although sporadic results are available: 13.4 mg/100 gr DW of ergosterol proxide in *M. esculenta* (Krzyczkowski et al., 2009), 28.6 mg/100 g brassicasterol, 1.23–4.54 mg/100 g campesterol and 2.44–12.3 mg/100 g of an unknown sterol (Phillips et al., 2011) (which together with campesterol detected exclusively in morels), 20.7– 32.6 mg/100 g FW ergosterol, 4.98–7.13 mg/100 g FW ergosta-5,7-dienol (22,23-dihydroergosterol), 4.39–6.26 mg/100 g D_2 (ergocalciferol) (Phillips et al., 2011), and 2.15–2.36 mg/100 g vitamin D_4 (22,23-dihydroergocalciferol) (Phillips et al., 2012). Other sterol compounds, including 5-dihydroergosterol, ergosterol peroxide, ergosterol and cerevisterol, were reported as anti-oxidative and anti-inflammatory compounds in *M. esculenta*, with IC_{50} values for NF-κB inhibitory activity of 5.2, 4.6, 2.0, and 5.1 μM, respectively (Kim et al., 2011).

Phenolic compounds

Some works have shown high correlation between anti-oxidative and anti-inflammatory capacity and phenolic contents in mushrooms, suggesting that phenolics, particularly phenolic acids, are the main anti-oxidants in mushroom (Cheung et al., 2003, Gursoy et al., 2009, Kalač, 2013, Taofiq et al., 2015)

Total phenolics content (TPC) of water and methanolic extracts of *M. conica* was reported as 16.9 and 4.6 mg GAE/g DW, while these of *M. anguisticeps* showed values of 13.1 GAE/g DW and 2.6 GAE/g DW for water and methanolic extracts, respectively (Puttaraju et al., 2006). However, Ramirez et al. determined TPC values of 45.9 mg/g DW and 173.5 mg/g DW in methanol and water extracts of *M. esculenta*, respectively (Ramírez−Anguiano et al., 2007). Other works also reported TPC of *M. conica*- Ozturk et al. reported values of 20.64 mg GAE/g in methanolic extracts (Ozturk et al., 2010), while Turkoglu et al. reported 41.93 μg/mg pyrocatechol equivalent in ethanolic extracts (Turkoglu et al., 2006). Mau et al. reported TPC of 3.63 mg/g in methanolic extracts of *M. esculenta* (Mau et al., 2004). Heleno et al. studied *M. esculenta* from Portugal and Serbia, showing 0.35 mg/100 g DW and 0.88 mg/100 g DW, respectively, also pronounced as 34.63 mg GAE/g extract and 32.17 mg GAE/g extract, respectively (Heleno et al., 2013). Vieira et al. reported TPC of *M. conica* from Portugal and Serbia, which showed values of 32.8 mg GAE/g extract and 26.4 mg GAE/g extract, respectively (Vieira et al., 2016). Gursoy et al. investigated the TPC of seven species of Morel, with results varying from 12.36 μg GAE/mg extract to 25.38 μg GAE/mg extract (Gursoy et al., 2009). The wide range of values and inconsistency between reports is referred to by many authors, and in most cases attributed to different origins, species, environmental conditions, maturity stage and extraction method.

Numerous works presented the phenolic acid profile of Morels; *M. conica* water extract contained 4.05 mg/g tannic and 12.85 mg/g gallic acid, while in *M. anguisticeps* 0.94 mg/g protocatechuic acid and 0.15 mg/g syringic acid were also reported, in addition to 8.63 mg/g tannic acid and 3.2 mg/g gallic acid (Puttaraju et al., 2006). Heleno et al. reported the phenolic acid profile of *M. esculenta* from Portugal and Serbia to include 0.24 mg/g and 0.06 mg/g protocatechuic acid, respectively, 0.1 mg/g (p-hydroxybenzoic acid), and 0.01 mg/g p-coumaric acid in Portuguese samples only (Heleno et al., 2013). Vieira et al. reported the profile of Portuguese and Serbian *M. conica* samples to include 20.8 mg/kg protocatechuic acid and 4.96 mg/kg protocatechuic acid, 2.48 mg/kg and 2.15 mg/kg p-coumaric acid, respectively and 55.2 mg/kg (p-hydroxybenzoic acid), 12.9 mg/kg cinnamic acid and 1.83 mg/kg gallic acid in Serbian samples only (Vieira et al., 2016). These results are in agreement with published phenolic profile of other edible mushrooms, showing generally the same phenolic acids as main phenolic compounds in mushrooms, with contents within the same range (Puttaraju et al., 2006, Barros et al., 2009, Heleno et al., 2015, Taofiq et al., 2015). Moreover, the main antioxidants in mushrooms are phenolic compounds (phenolic acids and flavonoids), while the antioxidative contribution of tocopherols, ascorbic acid and carotenoids is limited (Ferreira et al., 2009). Interestingly, Jander-Shagug et al. reported a correlation between mushroom's color and its phenols and anti-oxidants levels (Jander-Shagug and Masaphy, 2010).

Flavor

Morels' quality is attributed to their flavor, which is comprised of taste and aroma, as well as to their texture and color. Food taste perception is ascribed to soluble, nonvolatile compounds, while aroma is derived from volatile compounds. Mushrooms' flavor is unique to each type, and is subjected to changes, due to maturity stage, postharvest treatments and storage, and mainly due to drying processes (Wang et al., 2015, Yang et al., 2016).

Taste

The taste of edible mushrooms is primarily ascribed to several water-soluble substances, including 5′-nucleotides, free amino acids and soluble carbohydrates (Litchfield, 1967, Rotzoll et al., 2006, Pinho et al., 2008). In spite of their culinary importance and prized taste, not much information is available regarding morel's taste and aroma.

The main taste attributes of morels were described by a sensory trained-panel, using triangle tests, as 'bitter,' 'umami' ('monosodium glutamate (MSG)-like'), 'sour,' 'sweet,' 'salty' and 'mouth-drying' (Rotzoll et al., 2006), although other authors also mentioned 'tasteless' as an attribute, while omitting 'sour' and 'salty' attributes (Tsai et al., 2006, Beluhan and Ranogajec, 2011). Aiming at analyzing morel's taste non-volatile components, 33 putative taste compounds were detected, with specific compounds attributed to each taste component. Sweet perception in mushrooms was suggested earlier to result from the presence of soluble sugars (Litchfield, 1967, Tsai et al., 2006), and later on Rotzoll et al. also described some sweet-tasting free amino-acids as part of the sweet tasting compounds in *M. deliciosa*, to include mannitol, L-alanine, glucose, L-serine, L-threonine, ornithine, fructose, glycerin, glycine and L-proline (Rotzoll et al., 2006). These authors also listed sour/mouth drying compounds, including organic and amino-acids: γ-aminobutyric acid malic acid, citric acid, succinic acid, acetic acid, oxalic acid and L-lactic acid. Moreover, γ-aminobutyric acid

was specifically identified as the chemical inducer of morel's mouth-drying oral sensation (Rotzoll et al., 2006). Bitter-tasting compounds were mainly amino acids, including L-isoleucine, L-leucine, L-tyrosine, L-tryptophan, L-valine and hypoxanthine, while salts and amino acids imparted salty sensation: ammonia, potassium dihydrogenphosphate, sodium chloride, L-cysteine and L-methionine (Rotzoll et al., 2006).

Nevertheless, the predominant flavor of mushrooms is umami, which gives the most typical mushroom taste (Tsai et al., 2008). In mushrooms, umami taste was attributed to the levels of aspartic and glutamic acids, as well as to levels of 5′-nucleotides, which grant the characteristic MSG taste (Yamaguchi, 1979, Bellisle, 1999, Zhang et al., 2013). Aspartic and glutamic amino acids themselves provide a sour taste, whereas their sodium salts elicit the umami taste (Fuke and Shimizu, 1993). Specifically, umami taste in morel was attributed to adenosine-5′-monophosphate and uridine-5′-monophosphate, in addition to L-glutamic and L-aspartic acid (Rotzoll et al., 2006). Interestingly, (S)-morelid was detected as additional important umami-like taste compound, which also amplifies the sensation of MSG and sodium chloride (Rotzoll et al., 2006). Using taste omission and reconstitution tests, (S)-morelid, L-glutamic acid, L-aspartic acid, malic acid, citric acid, acetic acid and γ-aminobutyric acid were identified as the key organoleptics of morel extract (Rotzoll et al., 2006).

5′-Nucleutides contents in *M. elata* fruit body and *M. esculenta* mycelia were published, and results are presented in Table 2. Three most prominent nucleotides in mushroom flavor are termed "flavor 5′-nucleotides," to include 5′-guanosine monophosphate (5′-GMP), 5′-inosine monophosphate (5′-IMP) and 5′-xanthosine monophosphate (5′-XMP) (Beluhan and Ranogajec, 2011), with 5′-GMP giving the meaty flavor, and being a flavor enhancer much stronger than MSG (Litchfield, 1967). Among 10 Croatian wild edible mushrooms, high contents of flavor 5′-nucleotides was found in *C. cornucopioides* and in *M. elata* (5.32 mg/g) (Beluhan and Ranogajec, 2011). Particularly, the equivalent umami concentration (EUC) of mushrooms has been calculated, in order to understand their umami-like taste, due to its importance to mushroom sensory characteristics, overall flavor perception and consumer acceptance. EUC is the concentration of MSG equivalent to the umami intensity of a sample, which can be calculated according to the equation suggested by Yamaguchi et al. (1971). This value takes into account the relative contributions of umami amino acid (aspartic acid and glutamic acid), as well as the concentration of each flavor 5′-nucleotide- 5′-IMP, 5′-GMP, and 5′-XMP. Calculated EUC values for *M. elata* and *M. esculenta* were 97.52 g and 363.1 g MSG/100 g DW, respectively (Tsai et al., 2006, Beluhan and Ranogajec, 2011), while values of other mushroom types vary greatly (Kalač, 2016, Phat et al., 2016).

Table 2. Content of 5′-nucleotides of *M. elata* and *M. esculenta*.

	Content (mg/g dry weight)	
5′-nucleotides[a]	*M. elata*[b]	*M. esculenta*[c]
5′-AMP	6.57	0.67
5′-CMP	4.28	6.63
5′-GMP	1.19	1.65
5′-IMP	1.77	5.24
5′-UMP	4.19	6.08
5′-XMP	2.36	0.83

[a]5′-AMP- 5′-adenosine monophosphate; 5′-CMP, 5′-cytosine monophosphate; 5′-GMP, 5′-guanosine monophosphate; 5′-IMP, 5′-inosine monophosphate; 5′-UMP, 5′-uridine monophosphate; 5′-XMP, 5′-xanthosine monophosphate.
[b]Beluhan et al., *M. elata* fruit body, Croatia.
[c]Tsai et al., *M. esculenta* mycelium

Aroma

The characteristic aroma profile of mushrooms has been generally described, and consists of a few dozen volatile compounds of various chemical classes (Maga, 1981, Morath et al., 2012). These volatiles comprise of acids, alcohols, aldehydes, ketones, hydrocarbons, terpenes (mono and sesquiterpenes), furans and pyrans, pyrazines and sulfur compounds, with composition varies with species, maturity and growth conditions (Pinho et al., 2008, Aprea et al., 2015, Yang et al., 2016). Recently, some environmental and ecological roles were suggested for fungal volatiles, mainly in respect to environmental communication cues- mediating interactions between organisms within and across ecological niches and establish plant-fungal signals and interaction (Kramer and Abraham, 2012, Morath et al., 2012, Hung et al., 2015, Li et al., 2016).

Eight-carbon volatiles are ubiquitous among fungi, accounting for 44.3%–97.6% of the total volatile fraction (Combet et al., 2006), and have been reported to be the major contributors to characteristic mushroom flavor. Abundant mushroom-aroma C8 volatiles include 1-octen-3-ol, 1-octen-3-one, 2-octen-1-ol, 3-octanol, 1-octanol, 3-octanol, 3-octanone and (2E)-octenol (Fischer and Grosch, 1987, Venkateshwarlu et al., 1999, Cho et al., 2008, Tsai et al., 2009, Costa et al., 2013). In particular, 1-octen-3-ol, sensory described as of "mushroom-like" aroma (Mosandl et al., 1986), has been reported in many mushroom species in high concentrations (0.6–15.6 mg/100 g FW) (Kalač, 2009), and together with its oxidation product, 1-octen-3-one, is considered to be mainly responsible for the characteristic flavor of most edible species of mushrooms (Cho et al., 2006, Kalač, 2013). In addition to C8 volatiles, other key-odorant volatiles in mushroom include benzyl alcohol, benzahldehyde, phenylacetaldehyde and methional (Venkateshwarlu et al., 1999, Cho et al., 2006, Cho et al., 2008, Tsai et al., 2009, Costa et al., 2013).

Fungi utilize their fatty acids to produce volatile compounds, which is done by oxidation followed by cleavage, to produce short-chain volatiles (Vandamme, 2003, Combet et al., 2006). Linoleic acid is the most abundant fatty acid in mushrooms (63%–74%), followed by palmitic acid and stearic acid (Kalač, 2013). C8 compounds are synthesized in mushrooms through free linoleic acid oxidation, catalyzed by lipoxygenase and further cleavage of the intermediate by hydroperoxide lyase (Combet et al., 2006). Two mechanisms were suggested for this reaction, differentiate by the intermediate compound formed, proposed to be either 13-hydroperoxide (Tressl et al., 1982) or 10-hydroperoxide [(8*E*,12*Z*)-10-hydroperoxyoctadeca-8,12-dienoic acid] (Wurzenberger and Grosch, 1984), and although some investigations have been done, to-date the 1-octen-3-ol biosynthetic pathway is yet to be determined (Combet et al., 2006). Originating in polyunsaturated fatty acid oxidation, C8 compounds are classified as "oxylipins," and have been shown

to play a major role in biological processes in fungi, including development, cell growth, germination, sporulation, pathogenicity, apoptosis, reproductive events, and interactions with fungivores, pests and pathogens (Tsitsigiannis and Keller, 2007, Herrero-Garcia et al., 2011, Holighaus et al., 2014).

Volatile analysis of mushroom aroma was reported using various sampling methods, including, among others, simultaneous distillation extraction (SDE) (Jeleń, 2003), steam distillation, solvent extraction, dynamic headspace (purge & trap) and supercritical fluid extraction (SFE) (Combet et al., 2006, Yang et al., 2016). However, these methods are time consuming, sometimes involve use of organic solvents, might destroy delicate compounds and are not always representative of the headspace volatiles (Zhang and Li, 2010). Solid phase microextraction (SPME) is an adsorption/desorption technique which incorporates extraction, concentration and sample introduction into a single step. It is sensitive, reproducible, solvent-free (environmental- friendly) and cost efficient, and is thus nowadays preferred as a tool for aroma analysis sampling (Kramer and Abraham, 2012). Use of SPME for profiling fungal volatile metabolites has been widely reported since its introduction (Dıaz et al., 2003, Jeleń, 2003, Piloni et al., 2005, Da Costa et al., 2006, Politi et al., 2007, Pinho et al., 2008, Stoppacher et al., 2010, Lu et al., 2011, Costa et al., 2013, San Román et al., 2014, Aprea et al., 2015, Costa et al., 2015, Costa et al., 2015, Yang et al., 2016).

Despite their high importance, only one work examined the aroma profile of morels. This study described volatile profile of *M. esculenta* and *M. elata* from Turkey, using HS-SPME and GC-MS analysis. The profile of the two varieties differed, and comprised of a total of 31 identified aroma compounds, including 7 alcohols, 7 esters, 7 ketones, 3 acids, 2 aldehydes and 1 terpene (Taskin, 2013). Further studies are still required in order to establish the characterization of aroma profile of morels.

Conclusion and future prospective

Morel mushrooms are highly valued worldwide, owing to their attractive organoleptic characteristics and high nutritional value. Additionally, morels are consumed as a functional food, as they possess scientifically proven anti-oxidative, anti-inflammatory and immunostimulatory properties. Morels chemical composition was reported, including nutritional value, phytochemical and taste soluble components, whereas aroma was hardly investigated, and further research is required in order to establish our understanding of their aroma profile and key-odorants.

At the same time, it is important to be aware that morels are characterized by high plasticity in regard to metabolite levels and composition, and as a result in their bioactivity, affected by mushroom growth stage and by environmental conditions (Jander-Shagug and Masaphy, 2010, Masaphy et al., 2010, Heleno et al., 2013; Vieira et al., 2016,). This high phenotypic variability may also result in mis-identification of morel species when identified according to morphology. No molecular identification of the reported species is mentioned along with the biological activities described in the reviewed reports. In most of the reports, the authors have used the common species name, i.e., *M. esculenta* or *M. conica* (Table 1). The recent multigene molecular phylogenetic assessment approach (Kuo et al., 2012, Richard et al., 2015) suggested a revision in morel species taxonomy, while increasing the number of morel species based on molecular identification (Kuo et al., 2012). For example, the former identified *M. conica* species was found to actually include several genetic species: *M. deliciosa, M. purpurascens, M. tridentina* and *M. vulgaris* (Richard et al., 2015). Although it is difficult to correlate bioactive compounds composition and health effects with the exact morel genotype, since we are not always able to identify them, we are still able to compare the bioactivity of the Yellow and Black morel groups (i.e., the *Esculenta* clade and the *Elata* clade), since they are phenotypically different. Hence, the data obtained from the different reports might not be comparable and needs to be taken with caution. Further studies in this respect should include data on the molecular speciation, as well as additional data on the studied mushrooms, e.g., its growth stage, color, habitat etc., using same methodology in the different reports.

Another challenge in using morels as a functional food is that it is mostly obtained from wild growth, as morels are difficult to cultivate for mushroom production. Thus, an alternative way to exploit morel beneficial metabolites is by cultivation of Morchella species as fermented mycelia grown in liquid medium, and using their metabolites for consumption as functional food or for food flavoring. In Table 1, we have summarized the bioactivity studies of morels fruiting bodies and mycelial cultures. There is an increasing number of publications reporting investigations aiming to enhance bioactive metabolites production (especially polysaccharides) or to reduce cultivation costs by using low cost substrates, using different Morchella species. Yet, the main challenges of this cultivation system are repeatability, isolation and characterization of the active metabolites produced in liquid cultures, to compare with the ones produced by fruiting bodies and to prove their activity in vitro, and in vivo.

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