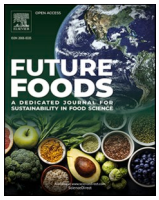
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Exploring the potential of saline mushrooms as a future food

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ABSTRACT

Environmental changes require agri-food systems to adapt. Moreover, recent nutritional guidelines also reflect aspects of sustainable production and healthy nutrition while respecting planetary boundaries. In this context, mushrooms which have beneficial nutritional properties, such as high protein content, and are rich in vitamins, trace elements, and secondary metabolites becoming the focus of research work. A next approach to cope with these challenges is to use extremophiles, that can adapt to changing environmental conditions such as high salinity. Therefore, the question arises as to which mushrooms can thrive in saline environments and be cultivated in future agri-food systems. Thus, this review aims to identify and evaluate the potential of saline mushrooms, including their nutritional properties and any possible toxicological risks. Eighty-six species of edible mushrooms that can live in saline environments were identified. Like other mushrooms, they contain high protein content. Moreover, these species were found to be rich in bioactive compounds such as phenolic compounds, tocopherols, ergosterol and polysaccharides. Several studies have also demonstrated their anti-carcinogenic, antioxidant and antimicrobial properties, indicating their potential as health promoters. This comprehensive review highlights the potential of saline mushrooms as a healthy protein-rich food in future diets. However, further research is essential to investigate the mechanisms behind the salinity tolerance of mushrooms and the influence of salinity on food quality and safety such as the accumulation of heavy metals or the production of toxins.

Introduction

Extreme weather events, such as droughts, floods, wildfires, and heat waves are on the rise due to climate change and destroying agricultural land, threatening food security and increasing hunger, poverty and malnutrition (World Meteorological Organization, 2024). One major issue is the increasing salinization of soil, which already affects 10.7 % (1.381 million hectares) of the total global land area and rendered it unfeasible to grow common crops (FAO, 2024). Despite extreme weather events, malnutrition and hunger remain significant problems alongside the rise in obesity and non-communicable diseases (NCDs) (WHO, 2022; Safiri et al., 2025). This highlights the necessity in the transformation of future diets and agri-food systems to become more healthy and sustainable for both humans and planet. More specifically, there are three key aspects: a diet should be diverse to provide all necessary nutrients and should maintain a healthy body weight, ensure biodiversity in the agri-food system; and keep the food system within planetary boundaries by avoiding wasting environmental resources (El Bilali, 2019; Lawrence, 2024). Seven of the nine planetary boundaries (climate change, biosphere integrity, land-system change, freshwater change, biogeochemical flows, ocean acidification, atmospheric aerosol loading, stratospheric ozone depletion, novel entities) have already been exceeded, including changes to freshwater and biosphere integrity (Richardson et al., 2023; Sakschewski et al., 2025).

Thus, there is an urgent need to explore new approaches to agricultural and food production. One approach is to search for extremophilic organisms that can withstand current and future environmental changes. Fungi are known to be extremophiles because they can cope with extremely high (thermophilic) and extremely low (psychrophilic) temperatures, acidic (acidophilic), alkaline (alkaliphilic), high salinity (halophilic), and extreme pressure (barophilic) conditions. This makes them an interesting target for research and industry. Halophilic organisms have the advantage of being able to be produced in a saline environment, thus exploiting new, previously unusable land such as salinized soils, and using saline water, thereby saving scarce fresh water, which accounts for only 3 % of the water on earth. This makes saline agriculture a promising field for future food production. Some fungi have been identified as growing in hypersaline environments. For

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example, *Aspergillus* spp., *Hortaea werneckii, Wallemia* spp., *Candida* spp., *Penicillium* spp., and *Cladosporium* spp. are known to be halophilic (Nina Gunde-Cimerman and Polona Zalar, 2014). However, all these fungi are microfungi and therefore of no interest in this context. So, the question arises: Are there edible macrofungi, referred as mushrooms, that are suitable for saline cultivation?

Mushrooms are eaten around the world, and the global mushroom trade reached $65.6 billion in 2024 and is estimated to grow to market size of $163.47 billion by 2034 (Bhilare, 2024). Of the estimated 2.2 to 3 million species of fungi, around 2200 species of wild edible fungi are known, 4.5 % of which are cultivated commercially (Pérez-Moreno, 2021; Rani et al., 2023). Another source says that about 7000 species have varying degrees of edibility (Kaliyaperumal et al., 2019). This natural resource, which has hardly been used to date, with the knowledge that mushrooms are highly nutritious and contain compounds with health-promoting properties moving them into the focus of current research work. They often have a higher protein content than vegetables combined with a richness of indispensable amino acids. They are also rich in carbohydrates and trace elements, as well as, vitamins A, B_1, B_2, B_3, B_5, C, and D_2, and secondary metabolites such as phenolic compounds, terpenoids, and steroids. Additionally, they are low in fat and cholesterol (Kaliyaperumal et al., 2019). Secondary metabolites are known to have health-promoting properties, such as anticarcinogenic, antidiabetic, and antioxidant properties, among others minimizing the risk of non-communicable diseases, such as diabetes or cardiovascular disease (Seca and Pinto, 2019; Wadhwa et al., 2024). There valuable nutritional profiles are one of the reasons why mushrooms are considered a promising future food (Bell et al., 2022). However, the accumulation of toxins and heavy metals in macrofungi can pose a health risk, which should not be neglected (Bucurica et al., 2024).

Despite extensive research on micro- and macrofungi, there is still no comprehensive overview of mushrooms that can be used in saline cultivation. So far, research on edible mushrooms has focused on nutritional aspects, such as bioactive compounds and health-promoting properties (Kumar et al., 2021; Seo and Choi, 2021; Venturella et al., 2021; Yadav and Negi, 2021; Zeb and Lee, 2021; Singh et al., 2025), as well as toxicological risks, such as toxin and heavy metal content (Govorushko et al., 2019; Yin et al., 2019; Wennig et al., 2020; Ab Rhaman et al., 2021; Liu et al., 2022). Some reviews have also addressed mushrooms as a potential food source, covering topics such as their use as an alternative protein, the farming of mushrooms to combat malnutrition and food scarcity, and the health benefits of incorporating them into the diet (Chatterjee et al., 2017; Ayimbila and Keawsompong, 2023; Khan et al., 2024; Ionescu et al., 2025; Liu et al., 2025; Michalska et al., 2025; Oh and Kim, 2025; Yuan et al., 2025). However, none of these reviews have addressed the potential of mushrooms cultivated in saline environments as an alternative food source. This review therefore provides a description of the terminology relating to saline mushrooms, identifies species of saline mushrooms, and evaluates their nutritional and toxicological properties. The nutritional properties of the identified species are described in terms of their nutritional value, bioactive compounds, and bioactivity. The toxicological properties include toxicological risks such as heavy metal content, toxins, and radioactive elements. This review provides a basis for further research into the cultivation of saline mushrooms and their potential to become part of a future diet.

What is a 'saline mushroom'?

The term 'saline mushrooms' has not yet existed. It should refer to edible macrofungi that can survive in saline environments and thus are suitable for saline cultivation. Edible fungi are macrofungi that develop fruiting bodies which can be consumed by humans and are referred to as mushrooms (Wei et al., 2022; Zou et al., 2023). The presence of toxic secondary metabolites, such as amatoxin, muscarine, and orellanine, as well as the indigestibility are the main criteria for classifying fungi as inedible (Li et al., 2021; Li et al., 2024; Ortiz-Letechipia et al., 2024, Troiano et al., 2020; Rani et al., 2023). One challenge in classifying edible fungi is the environmental variability with regard to biosynthesis and accumulation of toxins and morphological overlaps with toxic species. The accumulation of toxins is influenced by environmental and ecological factors such as substrate, and climate variability (Li et al., 2021; Li et al., 2024; Ortiz-Letechipia et al., 2024), resulting in fungi being classified as edible in one part of the world and inedible in another (Li et al. 2021). Some edible species, such as *Boletus edulis*, accumulate traces of toxins and heavy metals in polluted environments (Yan et al., 2023; Li et al., 2024). Another problem is the morphological overlap with toxic species. Genera such as *Amanita* and *Agaricus* have phenotypic similarities despite their differences in safety. This can lead to false identification and, consequently, intoxication, which is one of the leading causes of death due to mushroom poisoning (Li et al., 2021; Ortiz-Letechipia et al., 2024). Overcoming these challenges requires identifying a species based on a combination of genomic and ecological approaches, as well as sensory and instrumental analyses of toxic secondary metabolites. Methods such as DNA barcoding can distinguish between edible and toxic species (Li et al., 2021). To achieve full usability of the variety of edible saline mushrooms and advancing safety identification requires the development of portable, high-throughput, and on-site technologies (Wei et al., 2022).

Saline fungi can be classified as halophilic fungi, halotolerant fungi, halophiles, as well as marine fungi. Halophilic fungi have an obligate requirement for salt; halotolerant fungi can grow in saline conditions but do not require them. Halophiles are organisms adapted to high-saline environments (Jain et al., 2021). However, the definitions of halophilic and halotolerant fungi focus primarily on microfungi (N. Zhou et al., 2016; Tafer et al., 2019; Azpiazu-Muniozguren et al., 2021; Patankar et al., 2021; Wingfield et al., 2023), and no obligate halophilic macrofungi are known yet. Additionally, the distinction between obligate and facultative halophiles is inconsistent (Plemenitaš et al., 2014). There can be different ways of classifying saline macrofungi, such as by salinity tolerance or by habitat. Microfungi are classified by salt tolerance and are grouped into three categories: slight halophiles, which prefer a salt content of 0.3–0.8 M (1.7–4.8 %,); moderate halophiles, which prefer a salt content of 0.8–3.4 M (4.7–20 %); and extreme halophiles, which prefer a salt content of 3.4–5.1 M (20–30 %) (Ali et al., 2019). As a point of comparison, seawater has a salinity of around 0.5 - 0.6 M (approx. 3–3.5 %). However, this will not be feasible for macrofungi since the salinity tolerance will be lower. This suggests the need for new classification criteria for salt tolerance. As for classification by habitat, Stocker's classification system is applicable to halophytic plants, aqua-halines, terra-halines, and aero-halines (Stocker, 1933). Aqua-halines include marine fungi, which are species similar to fungi that grow in a marine environment (Jones et al., 2019). This brings us to terrestrial halophilic fungi. These fungi can grow in several terrestrial habitats, such as coastal dunes, coastal wetlands, inland wetlands, wooden dunes and others. Coastal dunes may comprise sandy soils, sand dunes, dune slack and grassland. As salinity depends on many factors, such as wave energy, wind direction, topology and vegetation, among others, the salinity range is wide (Du and Hesp, 2020). Salinity levels have been found to range from 0.5 to 50 dS m^{-1} (0.05–5 %) (Arulmathi and Porkodi, 2020). Wooded dunes are coastal dunes with more stable and sheltered conditions, supported by shrubs and trees. Here, salinity can range from 0.006 to 3 % (Langston et al., 2025). In coastal wetlands, including salterns and brackish wetlands, moderate to high salinity levels prevail (1 to 100 g l^{-1}, 1–10 %). Inland wetlands, including salt lakes and brines, have a high salinity of >100 g l^{-1}, >10 %. The salinity range is as follows: fresh water <1 g l^{-1} TDS, brackish water 1 to 10 g l^{-1} TDS, saline water 10 to 100 g l^{-1} TDS; and brine water >100 g l^{-1} TDS (van Weert et al., 2009), whereas TDS (total dissolved solids) describes the solids besides sodium chloride (salt), all major, trace, and ultra-trace minerals dissolved in one liter of water.

A saline mushroom must meet the criteria for edibility and salinity.

Since the evaluation of salinities is especially difficult in this review different criteria were developed to classify saline mushrooms and this review considers: A saline mushroom is an edible macrofungi, which can thrive in saline environments.

Material and methods

Literature search and selection

Firstly, an extensive literature search on saline fungi was conducted to identify saline mushrooms (Fig. 1). The following databases were used: Web of Science, Google Scholar, PubMed, and CORE. Search terms included "saline mushrooms" "edible saline fungi," "halophilic fungi," "salt-tolerant fungi," "edible halophytic fungi," "edible salt-loving fungi," "halophilic or halotolerant macrofungi," "salt AND fungi," and "fungi in saline environments." The following AI-based searching tools were also used: SciSpace, ORKG, Elicit, and Undermind. The search terms used were "What edible saline mushrooms exist?" and "What terrestrial fungi exist in coastal habitats?" "I want to find literature that identifies species of halophilic or halotolerant macrofungi thriving in saline environments." The literature search was conducted from May 2024 to May 2025. "Saline" was identified by either being categorized as halophilic or halotolerant or coming from a saline environment. This yielded a list of 516 species of saline fungi. To ensure no overlapping between marine fungi and macrofungi, 2572 species of macrofungi (Giblin and Legler, 2003) were compared to 2138 species of marine fungi (Jones et al., 2019) and no overlapping could be found. Secondly, the macrofungi were selected by excluding the microfungi, resulting in 159 species. Thirdly, salinity was categorized as S1 = known halotolerant, S2 = potential halotolerant, S3 = unknown. S1 describes halotolerant species that have been tested for salinity tolerance in laboratory experiments. S2 describes species that are potentially halotolerant because they grow in a saline environment categorized by proposed habitats (coastal dune habitat (CD), wooden dune habitat (WD), coastal wetlands (CW), inland wetlands (IW), indifferent (ID). Finally, S3 indicates that salt tolerance is unknown due to unclear habitat salinity. The salinity references are based solely on peer-reviewed publications. The 159 species were evaluated based on their edibility and categorized according to the following criteria: E1 = edible; E2 = potentially edible; E3 = discussed; E4 = unknown; and E5 = inedible. Firstly, E1 is based solely on peer-reviewed publications confirming their edibility. Secondly, E2 is based on Gray literature stating their edibility, which is indicated in the corresponding tables. Thirdly, E3 indicates that there are conflicting opinions about their edibility. Finally, no information on the edibility of E4 mushrooms could be found, and E5 mushrooms are stated as inedible. These categories resulted in lists of 86 edible (Table 1–3) and 74 inedible (Tables S1 and S2) species of macrofungi. The current names of the fungi species are listed.

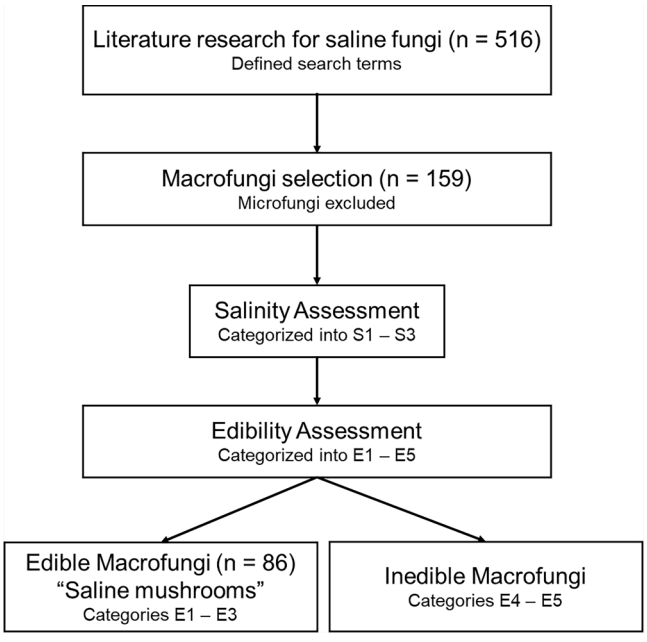


Fig. 1. Workflow for the identification and categorization of saline mushrooms. E1, edible; E2, potentially edible; E3, discussed; E4, unknown; and E5, inedible; S1, known halotolerant, S2, potential halotolerant, S3, unknown.

Results

Identification of saline mushrooms

To discuss the potential dietary use of saline mushrooms, it is first necessary to identify them in order to create a comprehensive overview. A total of 86 species were identified based on different criteria for salinity tolerance (S1-S3) and edibility (E1-E5). E1-E3 edibility levels are listed in Tables 1–3, respectively, while E4 and E5 are listed in Tables S1 and S2. As described previously, the salinity tolerance, if not S1, depends on the habitat. The proposed habitats were categorized as coastal dune habitat, wooden dune habitat, coastal wetlands, inland wetlands, or indifferent. Salinity increases in the following order: wooden dunes, coastal dunes, coastal wetlands, inland wetlands. The exact salinity ranges cannot be determined since they were not specified in the relevant publications.

First, the saline mushrooms are shown according to the edibility criterion E1. Fifty-three species were identified: Eight in salinity tolerance S1, 42 in S2, and three in S3. In terms of salinity tolerance S1, *S. bovinus* showed a salt tolerance up to 4 M NaCl, *S. luridus* and *S. luteus* up to 0.8 M NaCl, *R. roseolus* and *S. granulatus* up to 0.3 M and *P. ostreatus* up to 0.1 M of mycelia growth in media (Tang et al., 2009; Obase et al., 2010; Mousa, 2020; Nakano et al., 2022), while *P. tuber-regium* showed salinity tolerance of up 10 % NaCl (1.7 M) in the substrate (Ayodele and Ojoghoro, 2007). They are all edible, but some are considered conditionally edible. *A. rubescens, M. procera,* and *C. micaceus* contain coprine, a toxin that is only harmful when consumed with alcohol (Haberl et al., 2011). Some of the species must be cooked before eating since they contain thermolabile toxins, *A. rubescens* and *S. luridus*, and *B. utriformis* is edible only when young (Gerhardt, 1995). *S. commune* is the most widely distributed known mushroom in the world and therefore a high potential candidate for dietary use.

The following mushrooms meet the edibility criteria E2 for salinity (Table 2). The only notable species in terms of salinity tolerance is *M. xanthopus*, which can tolerate up to 3.5 % salinity (Castillo and Demoulin, 1997). In terms of edibility, *R. butyracea* has a poor taste, whereas *M. xanthopus* has a medicinal flavor (Gebreyohannes and Sbhatu, 2023).

The edibility of mushrooms category E3 is summarized in Table 3. *A. gemmate* is considered toxic by one reference (Fortunato Garza Ocañas et al., 2019) and edible by another (Kaliyaperumal et al., 2019), while *A. ovoidea* is considered edible by three references and poisonous by two (Martínez de Aragón et al., 2007; Doğan, 2013; Biagi et al., 2014; Li et al., 2021). Both are included in the *Amanitaceae* family, from which many poisonous mushrooms, such as *Amanita muscaria* (fly agaric), originate. *G. applanatum* is primarily used for medicinal purposes, although it is considered edible when cooked. *G. lucidum* is also used medicinally, particularly in the form of tea (Dimopoulou et al., 2022). *L. scrobiculatus* is considered poisonous by one reference, while considered edible by two (Martínez de Aragón et al., 2007; Joshi et al., 2013; Kaliyaperumal et al., 2019). No information is available for *L. vellereus* var. *hometii*. However, two sources consider *L. vellereus* inedible due its hard texture and poor taste (very hot and acrid) (First Nature, 2025; Wild Food UK, 2025), but it is considered edible by another

Table 1
Saline mushrooms with edibility category E1 (= edible). #Salinity tolerance (S1 = known halotolerant, S2 = potential halotolerant, S3 = unknown); CD, coastal dune habitat; WD, wooden dune habitat; CW, coastal wetlands; IW, inland wetlands; ID, indifferent.

Fungi species	Myco-bank taxon name ID*	Hab-itat	Salinity toler-ance#	Reference salinity tolerance	Reference edibility
Agaricus bernardii (Quél.) Sacc.	176,067	CD	S1	(Arora, 1986; Tóth, 2010; Evans and Roberts, 2015)	(Jiang et al., 2023)
Agaricus coniferarum Guinb. & Callac	820,478	CD	S2	(Moustafa, 1975; Smolskaite, 2016; Mahdizadeh et al., 2018)	(Smolskaite, 2016)
Agaricus devoniensis P.D. Orton	325,890	CD	S2	(Evans and Roberts, 2015; Smolskaite, 2016)	(Zhang, 2017)
Agaricus fissuratus (F.H. Møller)	292,263	WD	S3	(Smolskaite, 2016)	(Smolskaite, 2016)
Amanita rubescens	172,799	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Armillaria mellea (Vahl) P. Kumm.	190,066	CD	S2	(Zotti and Pautasso, 2013)	(Wu et al., 2012; Ren et al., 2023)
Boletus aereus	159,051	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Bovistella utriformis (Bull.) Demoulin & Rebriev	554,053	CD	S2	(Ghate and Sridhar, 2016)	(Frith-Macdonald et al., 2006; Ghate and Sridhar, 2016)
Cantharellus cibarius Fr.	200,345	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Clavulina coralloides (L.) J. Schroet.	114,573	CD	S2	(Zotti and Pautasso, 2013)	(Dann, 2016; Rasalanavho et al., 2019)
Clitocybe nebularis (Batsch) P. Kumm.	164,796	CW	S1	(Arora, 1986; Zotti and Pautasso, 2013; Azpiazu-Muniozguren et al., 2021)	(Li et al., 2021)
Clitopilus prunulus (Scop.) P. Kumm.	237,006	CD	S2	(Zotti and Pautasso, 2013; Georgieva et al., 2023)	(Arora, 1986; Alaimo et al., 2018)
Chlorophyllum rhacodes (Vittad.) Vellinga	374,433	CD	S2	(Ghate et al., 2014; Watling and Riddiford, 2021; Keleş and Genççelep, 2023)	Kaliyaperumal et al., 2019)
Collybia nuda (Bull.) Z.M. He & Zhu L. Yang	847,252	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007; Kaliyaperumal et al., 2019)
Coprinellus micaceus (Bull.) Vilgalys, Hopple & Jacq. Johnson	474,361	CD	S2	(Zotti and Pautasso, 2013)	(Orr et al., 1979)
Geopora arenicola (Lév.) Kers	283,460	CD	S2	(Zotti and Pautasso, 2013; Evans and Roberts, 2015)	(Lalotra et al., 2018)
Gyroporus castaneus (Bull.) Quél.	356,881	CD	S2	(Zotti and Pautasso, 2013)	(Valentão et al., 2005)
Helvella monachella (Scop.) Fr.	141,488	CD	S2	(Brain Douglas, 2016; Skrede et al., 2017)	(Acar et al., 2021)
Hydnum repandum L.	225,014	CD	S2	(Zotti and Pautasso, 2013)	(Phillips, Roger, Shearer, Lyndsay, Reid, Derek A.)
Laccaria laccata (Scop.) Cooke	119,173	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Lactarius chrysorrheus	233,874	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Lactarius subdulcis	201,988	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Leccinellum lepidum	104,996	CD	S2	(Zotti and Pautasso, 2013; Smolskaite, 2016)	(Kaliyaperumal et al., 2019)
Lentinus squarrosulus (Mont.)	477,648	ID	S2	(Ghate et al., 2014; Isikhuemhen et al., 2017)	(Kaliyaperumal et al., 2019)
Lycoperdon perlatum Pers.	220,647	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Macrolepiota procera (Scop.) Singer	287,857	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Marasmius oreades (Bolton) Fr.	174,712	CD	S2	(Arnolds, 1988; Tóth, 2010)	(Dimopoulou et al., 2022)
Mycena pura (Pers.) P. Kumm.	188,082	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Pleurotus citrinopileatus Sing.	303,973	CW	S2	(Li et al., 2023b)	(Kaliyaperumal et al., 2019; Dimopoulou et al., 2022)
Pleurotus djamor (Rumph. ex Fr.) Boedijn.	355,683	ID	S2	(Ghate et al., 2014)	(Ghate et al., 2014; Kaliyaperumal et al., 2019)
Pleurotus ostreatus (Jacq.) P. Kumm.	174,220	ID	S1	(Mousa, 2020; Keleş and Genççelep, 2023)	(Piska et al., 2017; Kaliyaperumal et al., 2019)
Pleurotus pulmonarius (Fr.) Quél.	143,543	IW	S2	(Kazantseva et al., 2024)	(Kaliyaperumal et al., 2019)
Pleurotus tuber-regium (Fr.) Singer	303,985	–	S1	(Ayodele and Ojoghoro, 2007)	(Ayodele and Ojoghoro, 2007)
Rhizopogon roseolus (Corda) Th. Fr.	100,130	CD	S1	(Zeller and Dodge, 1918; Matsuda et al., 2006; Nakano et al., 2022)	(Yun and Hall, 2004; Martínez de Aragón et al., 2007)
Russula chloroides (Krombh.) Bres.	193,143	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Russula cyanoxantha (Schaeff.) Fr.	190,250	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007; Kaliyaperumal et al., 2019)
Russula delica Fr.	184,527	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Russula heterophylla (Fr.) Fr.	193,557	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Russula nigricans Fr.	211,757	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Russula vesca Fr.	203,547	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Schizophyllum commune Fr.	208,403	CD	S2	(Zotti and Pautasso, 2013)	(Miller and Miller, 2006; Ruán-Soto et al., 2006)
Suillellus luridus (Schaeff.) Murrill	102,402	WD	S1	(Zotti and Pautasso, 2013; Smolskaite, 2016) (Tang et al., 2009)	(Kaliyaperumal et al., 2019)
Suillus bellinii (Inzenga) Watling	324,328	CD	S2	(Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007)
Suillus bovinus (L.) Roussel	356,928	WD	S1	(Tang et al., 2015)	(Martínez de Aragón et al., 2007; Kaliyaperumal et al., 2019)
Suillus granulatus (L.) Roussel	291,277	CD	S1	(Obase et al., 2010; Zotti and Pautasso, 2013)	(Martínez de Aragón et al., 2007; Kaliyaperumal et al., 2019)
Suillus luteus (L.) Roussel	120,823	WD	S1	(Tang et al., 2015)	(Miller and Miller, 2006; Martínez de Aragón et al., 2007; Kaliyaperumal et al., 2019)
Tricholoma columbetta (Fr.) P. Kumm.	155,124	CD	S2	(Smolskaite, 2016)	(Kaliyaperumal et al., 2019)

(*continued on next page*)

Table 1 (*continued*)

Fungi species	Myco-bank taxon name ID*	Hab-itat	Salinity toler-ance#	Reference salinity tolerance	Reference edibility
Tricholoma saponaceum (Fr.) P. Kumm.	186,494	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Tricholoma ustaloides Romagn.	307,065	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Volvariella volvacea (Bull.) Singer	307,802	CD	S2	(Zotti and Pautasso, 2013)	(Ali et al., 2024)
Xerocomellus chrysenteron (Bull.) Šutara	511,893	CD	S2	(Zotti and Pautasso, 2013)	(Arora, 1986)

* (Bensch, 2025)

Table 2
Saline mushrooms with edibility category E2 (= potential edible). #Salinity tolerance (S1 = known halotolerant, S2 = potential halotolerant, S3 = unknown); CD, coastal dune habitat; WD, wooden dune habitat; CW, coastal wetlands; IW, inland wetlands; ID, indifferent.

Fungi species	Myco-bank taxon name ID	Habi-tat	Salinity toler-ance#	Reference salinity tolerance	Reference edibility
Abortiporus biennis (Bull.) Singer	283,905	CD	S2	(Zotti and Pautasso, 2013)	(Goppa et al., 2023)
Aureoboletus gentilis (Quél.) Pouzar	326,828	CD	S2	(Zotti and Pautasso, 2013)	
Clitopilus geminus (Paulet) Noordel. & Co-David	509,887	CD	S2	(Zotti and Pautasso, 2013)	(First Naturec*)
Hygrophorus nemoreus (Pers.) Fr.	184,013	CD	S2	(Zotti and Pautasso, 2013)	
Hygrophorus russula (Schaeff.) Kauffman	102,423	CD	S2	(Zotti and Pautasso, 2013)	(Phillips, Roger, Shearer, Lyndsay, Reid, Derek A.)
Hypholoma lateritium (Schaeff.) P. Kumm.	455,825	CD	S2	(Zotti and Pautasso, 2013)	(Miller and Miller, 2006; Ványolós et al., 2020)
Lactarius atlanticus Bon	316,213	CD	S2	(Zotti and Pautasso, 2013)	(Simba, 2024)*
Lepista flaccida (Sowerby) Pat.	357,467	CD	S2	(Zotti and Pautasso, 2013)	(Bon, 1987)
Lepista multiformis (Romell) Gulden	115,280	CD	S2	(Evans and Roberts, 2015)	(Xu et al., 2024)
Leucopaxillus tricolor (Peck) Kühner	255,174	CD	S2	(Zotti and Pautasso, 2013)	(Geng et al., 2015)
Lycoperdon decipiens Durieu & Mont.	232,329	CD	S2	(Ghate and Sridhar, 2016)	(Ghate et al., 2014)
Melanoleuca bataillei Malençon	317,455	CD	S2	(Evans and Roberts, 2015)	(Kalmer İpek et al., 2022)
Microporus xanthopus (Fr.) Kuntze	456,171	CD	S1	(Castillo and Demoulin, 1997; Ghate and Sridhar, 2016)	(Ghate and Sridhar, 2016; Sholola et al., 2022)
Rhodocollybia butyracea (Bull.) Lennox	322,522	CD	S2	(Zotti and Pautasso, 2013)	(Phillips, Roger, Shearer, Lyndsay, Reid, Derek A; Wild Food UK, 2019)*
Russula badia Beeli	505,478	CD	S2	(Smolskaite, 2016)	(Burlingham, 1944; Smolskaite, 2016)
Russula graveolens Romell	193,504	CD	S2	(Zotti and Pautasso, 2013)	(Phillips et al., 2010)
Tricholoma atrosquamosum Sacc.	198,225	CD	S2	(Zotti and Pautasso, 2013)	(First Nature, n.d.d; Phillips, Roger, Shearer, Lyndsay, Reid, Derek A.)*
Xerocomellus pruinatus (Fr.) Šutara	511,898	CD	S2	(Zotti and Pautasso, 2013)	(First Nature, n.d.e; Pecina et al., 2022)*

* Gray literature is indicated in grey.

(Kaliyaperumal et al., 2019). The *P. hadriani* is described being edible when it is in its egg form. Additional to the sources describe them edible (Table 3), *P. arhizus* and *R. emetica* are described as poisonous (Phillips, Roger, Shearer, Lyndsay, Reid, Derek A; Martínez de Aragón et al., 2007; Niedzielski et al., 2023; Niedzielski et al., 2024). *T. versicolor* is described as inedible due to the hardness of its flesh. However, it is also proposed for use as an alternative to chewing gum and for medicinal purposes. *H. rubellus* is considered inedible because of its soapy taste.

Considering the habitats in which they were found, it was determined that 79 % of the saline fungi identified inhabited coastal areas. Most of these were found in sand dunes and sandy soil (Fig. S1). The remaining 21 % were found to inhabit wooden dunes, indifferent habitats, coastal wetlands and inland wetlands. Wooden dunes (7 %) were mostly sandy woods and pine forests. Indifferent habitats (10 %) comprised termite mounds, bark, willow, wood stumps, wood substrates, and fungi grown on substrates/media. Coastal wetlands (2 %) were found to consist of brackish water and salterns. Inland wetlands represented only 1 % and consisted of salt lakes.

In terms of fungal species systematics, *Russulaceae* is the most abundant family, accounting for 17 % of species, followed by *Agaricaceae* and *Boletaceae* (8 %), *Tricholomataceae* (7 %), *Pleurotaceae* (6 %), *Clitocybaceae* and *Suillaceae* (5 %), *Amanitaceae, Hydnaceae, Lycoperdaceae* and *Polyporaceae* (3 %), and all others combined accounting for 1–2 % (Fig. 2), whereas the *Agaricaceae, Boletaceae, Russulaceae* and *Tricholomataceae* families comprise the most edible species (Kaliyaperumal et al., 2019).

Nutritional properties of selected saline mushrooms

When considering saline mushrooms as a food source, it is crucial to examine their nutritional properties. Since nearly no studies on mushrooms from saline cultivation are available so far, the following chapters on nutritional properties and toxicological aspects are limited to studies from classical cultivation or wild mushrooms. Of the 53 species identified under edibility criterion E1, the chemical and bioactive compounds of 28 species were studied. These studies identified specific compounds in these mushrooms, but a comprehensive analysis of their nutritional profiles is lacking. In terms of macronutrients, fungi are of particular interest due to their high protein content. This was found to be lowest at 8 g 100 g^{-1} DW in *B. aereus* (Stojković et al., 2015), and highest at 50 g 100 g^{-1} DW in *L. squarrosulus* (Ugbogu et al., 2024). In *C. cibarius, V. volvacea, S. bovinus, P. pulmonarius, P. citrinopileatus, L. perlatum, C. nuda, G. arenicola, S. luridus* values between 20 – 30 g 100 g^{-1} DW were found (Barros et al., 2008; Liu et al., 2016; Raman et al., 2020; Dimopoulou et al., 2022; Ali et al., 2024). These values are comparable to those of mushrooms from classic cultivation, for example, the protein content is

Table 3
Saline mushrooms with edibility category E3 (= discussed). #Salinity tolerance (S1 = known halotolerant, S2 = potential halotolerant, S3 = unknown); CD, coastal dune habitat; WD, wooden dune habitat; CW, coastal wetlands; IW, inland wetlands; ID, indifferent.

Fungi species	Myco-bank taxon name ID	Habi-tat	Salinity tolerance*	Reference salinity tolerance	Reference edibility
Agaricus xanthoderma var. *lepiotoides* Maire	116,881	CD	S2	(Zotti and Pautasso, 2013)	(La Rosa et al., 2024)
Amanita gemmata (Fr.) Bertill.	202,929	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Amanita ovoidea (Bull.) Link	156,329	WD	S2	(Zotti and Pautasso, 2013; Smolskaite, 2016)	(Martínez de Aragón et al., 2007; Doğan, 2013; Biagi et al., 2014; Li et al., 2021)
***Dacrymyces spathularia* (Schwein.) Alvarenga**	841,Simba256	WD	S3	(Ghate and Sridhar, 2016; Alvarenga and Xavier-Santos, 2017)	(Ghate et al., 2014)
Ganoderma applanatum (Pers.) Pat.	119,872	ID	S2	(Ghate and Sridhar, 2016)	(Ghate and Sridhar, 2016)
Ganoderma lucidum (Fr.) P. Karst.	148,413	ID	S2	(Zotti and Pautasso, 2013; Ghate and Sridhar, 2016)	(Ghate and Sridhar, 2016)
Hortiboletus rubellus (Krombh.) Simonini	551,214	CD	S2	(Zotti and Pautasso, 2013)	(First Naturea)*
Lactarius scrobiculatus	196,637	CD	S2	(Zotti and Pautasso, 2013)	(Joshi et al., 2013; Kaliyaperumal et al., 2019)
Lactarius vellereus var. *hometii* (Gillet) Boud.	200,943	CD	S2	(Zotti and Pautasso, 2013)	
Lactarius vinosus Quél.	456,055	CD	S2	(Nuytinck and Verbeken, 2003; Smolskaite, 2016)	(Smolskaite, 2016)
Phallus hadriani	245,853	CD	S2	(Evans and Roberts, 2015)	(First Nature, n.d.b; MykoWeb, n.d; Bolesławska et al., 2024)*
Pisolithus arhizus (Scop.) Rauschert	276,857		S1	(Matsuda et al., 2006)	(Razzaq and Shahzad, 2004)
Russula emetica (Schaeff.) Pers.	191,650	CD	S2	(Zotti and Pautasso, 2013)	(Kaliyaperumal et al., 2019)
Tricholoma equestre (L.) P. Kumm.	198,108	CD	S2	(Smolskaite, 2016)	(Smolskaite, 2016; Rzymski and Klimaszyk, 2018; Oba et al., 2024)
Trametes versicolor (L.) Lloyd	281,625	CD	S2	(Zotti and Pautasso, 2013)	(Midwest Mycology, n.d; Ajibola et al., 2024)*

* Gray literature is indicated in grey.

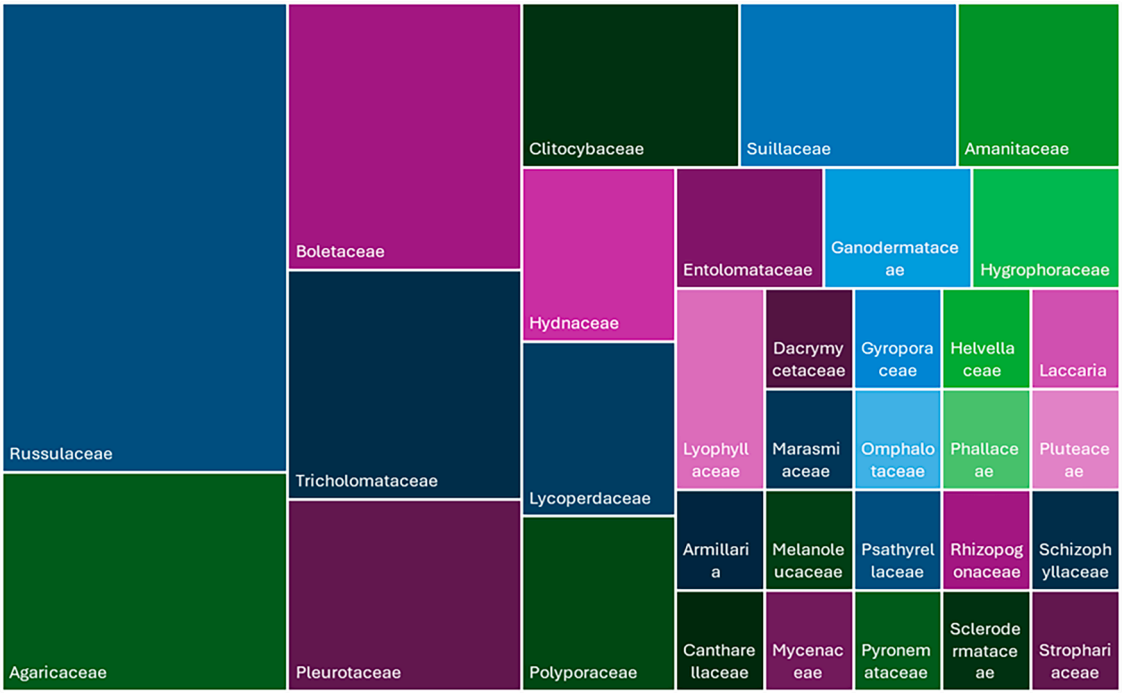


Fig. 2. Distribution of plant families of saline mushrooms. N = 86 (Tables 1–3).

between 32 g 100 g DW for *A. bisporus* (button mushroom), 20 g 100 g DW for *P. ostreatus* (oyster mushroom), 22.8 g 100 g DW for *L. edodes* (shiitake mushroom) and 20 g 100 g DW for *F. velutipes* (Enoki mushroom) (Singh et al., 2025). Mushrooms can be considered as an alternative source of dietary protein. The recommended daily protein intake for a healthy adult is 0.8 g per kg of body weight (Wu, 2016). With an average adult body weight of 62 kg (Walpole et al., 2012), the daily requirement would be 49.6 g protein. Assuming an average protein content of 30 %, only 165 g of mushrooms (equivalent to approximately seven average-sized button mushrooms) would need to be consumed to reach the recommended daily protein intake. By comparison, you would need to eat 190 g of ground beef, which contains 26 g of protein per 100 g (USDA, 2019). Besides having a high protein content, they also have a balanced amino acid profile containing all the essential amino acids, as demonstrated for *A. rubescens, S. luteus* and *S. granulatus* (Riberio et al., 2008). Next to protein content, another important macronutrient class is

carbohydrates. The lowest total carbohydrate content was found to be 10 g 100 g^{-1} DW for *C. nuda* (Barros et al., 2008), while the highest was found to be 81 g 100 g^{-1} DW for *P. ostreatus* (Deveci et al., 2019). This is comparable again to cultivated mushrooms. The respective carbohydrate contents of *A. bisporus, P. ostreatus, C. cibarius* and *B. edulis* are 63 g, 50 g, 65 g and 46 g per 100 g of dry weight (DW) (Fogarasi et al., 2018). Mushroom carbohydrates consist of hexoses, methylpentoses, amino sugars, disaccharides, sugars, acids and sugar alcohols (Kaliyaperumal et al., 2019). Polysaccharides, including chitin, are also important carbohydrates in mushrooms due to their bioactivity, which will be described below. Compared to the other macronutrient groups, fat content was found to be present in small quantities, at around 2 % (Dimopoulou et al., 2022). Which is in accordance with mushrooms from classical cultivation (Kalac, 2016). As well as macronutrients, fungi are a good source of micronutrients, including main elements such as potassium, calcium, magnesium, phosphorus and sodium; trace elements such as iron, manganese, molybdenum, zinc and copper; ultra-trace elements such as aluminum and arsenic; and bioactive compounds, which will be described in more detail in the following (Kaliyaperumal et al., 2019).

Bioactive compounds are of special interest when it comes to evaluating the nutritional properties related to health, due to their health-promoting properties. Of the 60 studies and 28 fungal species involved, 31 studies revealed the abundance of phenolic compounds, 12 studies highlight the abundance of ergosterol, and 12 studies include information about tocopherols or carotenoids. Six studies comprise polysaccharides (Table 4). Phenolic compounds include phenolic acids, such as cinnamic acid and *p*-hydroxybenzoic acid, as well as flavonoids, such as catechin and quercetin. These compounds have health-promoting properties, including anti-carcinogenic, anti-inflammatory, neuroprotective and antimicrobial properties (Wadhwa et al., 2024). The total phenolic content, measured in gallic acid equivalents (GAE), was found to range from 1.75 mg GAE g^{-1} in *C. cibarius* (Barros et al., 2009) to 20.93 mg GAE g^{-1} in *A. rubescens* (Tapan et al., 2024). The average content is at 8 mg GAE g^{-1} (Barros et al., 2009; Gursoy et al., 2010; Guo et al., 2012; Smolskaitė et al., 2015; Akata et al., 2019; Shomali et al., 2019; Kostić et al., 2020). Ergosterol is a sterol found in fungi and is the precursor of vitamin D_2. A UV-induced reaction leads to the transformation of ergosterol into vitamin D_2. Therefore, considering the worldwide prevalence of vitamin D_2 deficiency, the abundance of ergosterol is of high interest (Amrein et al., 2020). Several studies have detected ergosterol abundance. Although values varied considerably between species - for example, the values shown for *L. perlatum, M. procera, R. delica* and *S. bovinus* were 79.4, 191, 16.9 and 123 mg^{-1} 100 g FW, respectively (Carvalho et al., 2014). A recent randomized controlled trial (4-week parallel design, n = 36) supported the beneficial effect of consuming vitamin D_2-enriched mushrooms. The trial showed that consuming vitamin D_2-enriched *P. citrinopileatus* led to higher serum levels of 25-hydroxyvitamin D_2, the bioactive form of vitamin D_2 (Hsu et al., 2025). Polysaccharides are polymers of monosaccharides. The most abundant monosaccharides in mushrooms are arabinose, xylose, mannose, glucose and galactose (Zhang et al., 2018; Deveci et al., 2019). Polysaccharides were shown to have health-promoting properties, such as antioxidant activity involving the scavenging of reactive oxygen species (ROS) (Mu et al., 2021; Li et al., 2023c). The total polysaccharide content ranges from 2.75 to 9.27 mg glucose g^{-1} DW in the following species: *A. mellea, P. citrinopileatus, P. ostreatus, S. bovinus, V. volvacea* and *C. cibarius* (Guo et al., 2012).

A total of 58 studies on the bioactivity of saline mushrooms were found (see Table 5). The majority of these studies focused on *S. commune*, followed by *M. procera, C. nuda*, and *A. mellea* (Fig. S2). Most of the studies (88 %) were in vitro, using fungal extracts or specific extracts of compounds such as polysaccharides on carcinogenic cell lines. 7 % were in vivo studies and animal trials, mostly involving mice, and only 3 % were human intervention trials (Fig. S3). Many of the in vitro studies tested the antioxidant capacity using TEAC, FRAP, DPPH or

Table 4
Chemical and bioactive compounds of selected saline mushroom species belonging to category E1, as defined in Table 1.

Mushroom	Compound	References
Armillaria mellea	Adenosine, alanine, ascorbic acid, cinnamic acid, D-galactose, ergosterol, ferulic acid, flavonoids, gallic acid, glycerol, linoleic acid, oleic acid, paraben, petroselinic acid, phenols, polysaccharides (consist primarily of glucose (90.48 %)), protocatechuic acid, pyroglutamic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, serotonin, syringic acid, threonine, tocopherols, tryptamine, tryptophan, vanillic acid	(Erbiai et al., 2023) (Li et al., 2022) (Wu et al., 2012) (Lung and Chang, 2011) (Reczyński et al., 2013)
Boletus aereus	Citric acid, cinnamic acid, fumaric acid, hydroxybenzoic acid, oxalic acid, *p*-coumaric acid, quinic acid, tocopherols	(Stojković et al., 2015)
Bovistella utriformis	Bioactive peptides	(Landi et al., 2022)
Cantharellus cibarius	5-Hydroxytryptophan, ascorbic acid, β-carotene, cinnamic acid, flavonoids, indole-3-acetonitrile, kynurenine sulphate, lycopene, melatonin, *p*-hydroxybenzoic acid, phenols, protocatechuic acid, serotonin, sinapinic acid, tocopherols, tryptamine, tryptophan, vanillic acid	(Muszynska et al., 2013) (Barros et al., 2009) (Barros et al., 2008) (Muszyńska and Sułkowska-Ziaja, 2012)
Clitocybe nebularis	Lectin (*C. nebularis* lectin), sesquiterpenoids (nebucanes A – G)	(Svajger et al., 2011; Sabotič and Kos, 2019; Schrey et al., 2022)
Clitopilus prunulus	Polyamines (putrescine and spermidine)	(Rašeta et al., 2024)
Chlorophyllum rhacodes	Cinnamic acid, linoleic acid, malic acid, mannitol, oleic acid, oxalic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, palmitic acid, tocopherols (α-tocopherol and β-tocopherol), trehalose	(Ćirić et al., 2019)
Collybia nuda	Ascorbic acid, β-carotene, caffeic acid, catechin, chlorogenic acid, cinnamic acid, ellagic acid, ferulic acid, flavonoids, gallic acid, hydroxybenzoic acid, lycopene, methylparaben, *p*-coumaric acid, *p*-hydroxybenzoic acid, phenols, polyamines (major spermidine and putrescine), protocatechuic acid, serotonin, sinapinic acid, syringic acid, tocopherols, tryptamine, tryptophan, vanillic acid	(Erbiai et al., 2023) (Rašeta et al., 2024) (Barros et al., 2009) (Barros et al., 2008)
Gyroporus castaneus	Citric acid, fumaric acid, ketoglutaric acid, malic acid, succinic acid	(Valentão et al., 2005)
Hydnum repandum	Caffeic acid, cinnamic acid, coumaric acid, coumarin, ellagic acid, ferulic acid, fumaric acid, gallic acid, gentisic acid, hydroxybenzoic acid, indole, melatonin, *p*-coumaric acid, *p*-hydroxybenzoic acid, protocatechuic acid, rosmarinic acid, serotonin, sinapinic acid, syringic acid, *trans*-2-hydroxycinnamic acid, *trans*-cinnamic acid, tryptamine, tryptophan, vanillic acid	(Çayan et al., 2021) (Sułkowska-Ziaja et al., 2015)
Laccaria laccata	Anthranilic acid derivatives, laccanthrilic acids A, B, and C ((3S)-1,2,3,4-tetrahydro-3-β-carboline-3-carboxylic acids)	(Schrey et al., 2019) (Oberemko et al., 2019)
Lactarius chrysorrheus	Polysaccharides	(Mutlu et al., 2022)
Lentinus squarrosulus	Eicosene, ergosterol, fumaric acid, octahydropyrrolo[1,2-a]pyrazine, phytol, 1-tetradecene, 6-ethyloct-3-yl ester	(Ugbogu et al., 2024)

(*continued on next page*)

Table 4 (*continued*)

Mushroom	Compound	References
Lycoperdon perlatum	Ascorbic acid, β-carotene, cinnamic acid, ergosterol, flavonoids, lycopene, lycoperdic acid (4-hydroxyglutamic acid derivate), phenols, tocopherols	(Barros et al., 2009) (Barros et al., 2008) (Katsuta et al., 2021) (Carvalho et al., 2014)
Macrolepiota procera	Adenosine, alanine, α-tocopherol, β-tocopherol, β-carotene, cinnamic acid, citric acid, D-galactose, ergosterol, ferulic acid, fumaric acid, gallic acid, lepiotaprocerins a–l, linoleic acid, lycopene, lycoperdic acid (4-hydroxyglutamic acid derivate), malic acid, mannitol, oleic acid, oxalic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, palmitic acid, paraben glycerol, petroselinic acid, phenols, pidolic acid, protocatechuic acid, syringic acid, threonine, tocopherols, trehalose, tryptophan, vanillic acid	(Chen et al., 2018) (Erbiai et al., 2021) (Ćirić et al., 2019) (Barros et al., 2009)
Marasmius oreades	Catechin, ferulic acid, gallic acid, vanillic acid	(Shomali et al., 2019)
Pleurotus citrinopileatus	Ascorbic acid, α-tocopherol, β-carotene, chlorogenic acid, homogentisic acid, *p*-hydroxybenzoic acid, phenols, polysaccharides	(Lee et al., 2007) (Guo et al., 2012)
Pleurotus ostreatus	1-Octen-3-ol3-octanone, 5-hydroxy-tryptophan, α-tocopherol, ascorbic acid, β-carotene, cinnamic acid, chlorogenic acid, ferulic acid, indole acetonitrile, indoleacetic acid, linolenic acid, niacin, oleic acid, *p*-hydroxybenzoic acid, protocatechuic acid, riboflavin, serotonin, sinapinic acid, thiamine, tryptamine, tryptophan, vitamin B_{12}, vitamin C	(Piska et al., 2017) (Muszyńska and Sułkowska-Ziaja, 2012) (Zhang et al., 2008) (Muszynska et al., 2013)
Russula chloroides	Ferulic acid, gallic acid, myricetin	(Kostić et al., 2020)
Russula cyanoxantha	Ceramide (phytosphingosine/α-fatty acid; (2S,3S,4R,2′R)-2-(2′-hydroxytetracosanoylamino) octadecane-1,3,4-triol), ergosterol derivates	(Gao et al., 2001)
Russula delica	Chrysin, ergosterol, ferulic acid, *o*-coumaric acid, oleanolic acid, *p*-hydroxybenzoic acid, *p*-hydroxyphenylacetic acid, ursolic acid	(Carvalho et al., 2014) (Kalogeropoulos et al., 2013)
Schizophyllum commune	Adenine, catechin, catechin-hydrate, ergosterol, ergosterol peroxide, ferulic acid, fumaric acid, α-glucan, β-glucan, gallic acid, genistein-4,7-dimethyl ether, isorhamnetin, morusin, phloretin, poricoic acid g, quercetin, syringic acid, trehalose	(Çayan et al., 2021) (Chen et al., 2024) (Klaus et al., 2011)
Suillus bellinii	Chrysin, cinnamic acid, ergosterol, ferulic acid, *o*-coumaric acid, oleanolic acid, *p*-hydroxybenzoic acid, *p*-hydroxy phenylacetic acid, protocatechuic acid, ursolic acid	(Kalogeropoulos et al., 2013) (Souilem et al., 2017)
Suillus bovinus	Chitosan, ergosterol, gallic acid, homogentisic acid, *p*-hydroxybenzoic acid, polysaccharides, protocatechuic acid	(Oberemko et al., 2019) (Carvalho et al., 2014) (Guo et al., 2012)
Suillus granulatus	Suillin (4-acetoxy-3-geranylgeranyl-1,2-dihydroxybenzene), tetraphenyl phenols, polysaccharides	(Tringali et al., 1989b) (Tringali et al., 1989a) (Gao et al., 2022)(Zhou et al., 2016b)
Tricholoma ustaloides	Saponaceolides, tricholidic acids and tricholomenyn C	(Gilardoni et al., 2023a)
Volvariella volvacea	Gallic acid, 1-octen-3-ol, 3-octanone, polysaccharides, β-glucan, zymosan, flammotoxin, volvatoxin, 2-pyrrolidinones	(Guo et al., 2012) (Zhang et al., 2008) (Ali et al., 2024) (Bai et al., 2021)
Xerocomellus chrysenteron	Citric acid, fumaric acid, ketoglutaric acid, malic acid, succinic acid	(Valentão et al., 2005)

Table 5
The bioactivity of the selected saline mushroom species belonging to category E1 is shown in Table 1.

Mushroom	Bioactivity	Experimental model	References
Armillaria mellea	Antioxidant activity	*in vitro*	(Erbiai et al., 2021) (Lung and Chang, 2011)
	Polysaccharide extract improves learning and memory, antioxidant properties, neurotransmitter modulation and neuroprotective effects in a D-galactose-induced ageing mouse model	*in vivo*	(Li et al., 2022)
	Water extract shows antidepressant-like (in both acute stress (FST) and chronic stress (UCMS) models), anti-inflammatory (antidepressant effects were associated with anti-inflammatory effects) and downregulated inflammatory cytokines (such as IL-1β and TNF-α) and neurotransmitter activity (modulated serotonin (5-HT) turnover in the brain) in rodents	*in vivo*	(Lin et al., 2021)
	Anti-cancer activity against A549 lung cancer cells by inducing cell cycle arrest, apoptosis and mitochondrial dysfunction	*in vitro*	(Wu et al., 2012)
Boletus aereus	Antioxidant, antimicrobial; extract controlling microbial growth in pork meat	*in vitro*	(Stojković et al., 2015)
	Polysaccharide called BAPN-1, anti-proliferative effects against various non-Hodgkin's lymphoma (NHL) cell lines	*in vitro*	(Wang et al., 2024)
Cantharellus cibarius	Isolated polysaccharides show anti-cancer activity against human colon cancer cells	*in vitro*	(Lemieszek et al., 2019)
	Selective antimicrobial activity against gram-positive bacteria such as *Bacillus subtilis* and *Staphylococcus aureus*	*in vitro*	(Barros et al., 2008)
	Ethanolic extracts showed cytotoxic effects against glioblastoma cell lines	*in vitro*	(Nowakowski et al., 2021)
Chlorophyllum rhacodes	Antioxidant, antifungal and antibacterial (Methicillin-resistant *Staphylococcus aureus* and *Escherichia coli*) effects	*in vitro*	(Ćirić et al., 2019)

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Table 5 (*continued*)

Mushroom	Bioactivity	Experimental model	References
Clavulina coralloides	Isolated lectin CNL has an immunostimulatory effect	*in vitro*	(Svajger et al., 2011)
Clitocybe nebularis	GalNAcβ1–4GlcNAc-binding lectin shows selective antiproliferative activity	*in vitro*	(Perišić Nanut et al., 2022)
Collybia nuda	Polysaccharides LNP-1 and LNP-2 have antioxidant activity (cellular antioxidant activity (CAA) assay using HepG2 cells), antitumor (anti-proliferative effects on A375 melanoma cells) and immunomodulatory (induced macrophages (RAW264.7 cells) to secrete immunomodulatory factors including nitric oxide (NO), TNF-α and IL-6) effects	*in vitro*	(Li et al., 2023c)
	Antioxidant activity, antimicrobial activity (pathogenic bacteria including *Micrococcus luteus, Staphylococcus aureus, Bacillus cereus, Yersinia enterocolitica, Salmonella enteritidis* and *E. coli*)	*in vitro*	(Mercan et al., 2006)
	Neuroprotective effects (anti-acetylcholinesterase activity) (99.94 % inhibition rate)	*in vitro*	(Rašeta et al., 2024)
	Selective antimicrobial activity against Gram-positive bacteria such as *Bacillus subtilis* and *Staphylococcus aureus*	*in vitro*	(Barros et al., 2008)
Hydnum repandum	Antioxidant activity, α-amylase inhibitory activity	*in vitro*	(Çayan et al., 2021)
	Antibacterial properties	*in vitro*	(Karakas et al., 2023)
Laccaria laccata	Laccanthrilic acid B showed moderate nematocidal activity against *Caenorhabditis elegans*	*in vitro*	(Schrey et al., 2019)
	Chitosan films show a concentration-dependent effect on cancerous hepatoma (MH-22A) and non-cancerous ovary (CHO), necrosis and apoptosis-like processes	*in vitro*	(Oberemko et al., 2019)
Lactarius chrysorrheus	Polysaccharide extract anticancer agent targeting HepG2 and PANC-1 cell lines by inhibiting cell migration, colony formation and inducing apoptosis	*in vitro*	(Mutlu et al., 2022)

Table 5 (*continued*)

Mushroom	Bioactivity	Experimental model	References
Lentinus squarrosulus	ROS scavenging, antioxidant, antimicrobial, anticancer	*in vitro*	(Ugbogu et al., 2024)
Lycoperdon perlatum	Antimicrobial activity (*Candida albicans* and *Cryptococcus neoformans*)	*in vitro*	(Barros et al., 2008)
	Ethanolic extracts showed cytotoxic effects against glioblastoma cell lines	*in vitro*	(Nowakowski et al., 2021)
Macrolepiota procera	Lepiotaprocerin extract shows anti-inflammatory (inhibition of nitric oxide production in RAW 264.7 macrophages), anticancer (cytotoxicity against several human cancer cell lines, including HL-60 (leukemia), A-549 (lung cancer), SMMC-7721 (hepatocellular carcinoma), MCF-7 (breast cancer) and SW-480 (colon cancer)) and antimycobacterial (antitubercular activity, with an MIC (minimum inhibitory concentration) of 50 μg mL^{-1} against *Mycobacterium tuberculosis* H37Ra) properties	*in vitro*	(Chen et al., 2018)
	Antioxidant activity, antifungal and antibacterial (MRSA and *E. coli.*) effects	*in vitro*	(Erbiai et al., 2021) (Ćirić et al., 2019)
	Polysaccharide extract showed immunomodulatory (increased the number of CD14+ monocytes in human blood and activated the oxidative burst in phagocytes; induced NO and interleukin production by macrophages), probiotic (promoted the growth of probiotic strains such as *Lactobacillus spp.* and *Clostridium beijerinckii*) and antimicrobial (inhibited pathogens such as *E. coli, Streptococcus mutans* and *Salmonella enterica*) effects	*in vitro*	(Georgiev et al., 2022)
Marasmius oreades	Antibacterial properties	*in vitro*	(Karakas et al., 2023)
Pleurotus citrinopileatus	Water extracts containing polysaccharides and phenols have anti-obesity, hypolipidaemic and	*in vitro*	(Sheng et al., 2019)

(*continued on next page*)

Table 5 (*continued*)

Mushroom	Bioactivity	Experimental model	References
	glucose-regulating properties		
	Polysaccharide has antitumor and immunomodulatory properties on H22-tumor bearing mice	*in vivo*	(Wang et al., 2021)
	Vitamin D-enriched *P. citrinopileatus* increased serum vitamin D (25(OH)D) levels	Human intervention trial	(Hsu et al., 2025)
Pleurotus ostreatus	Antimicrobial effects	*in vitro*	(Smolskaitė et al., 2015)
	Anti-cancer and thrombolytic activity, tyrosinase and α-glucosidase inhibition	*in vitro*	(Sharif et al., 2018)
	Antioxidant activity	*in vitro*	(Zhang et al., 2008)
Rhizopogon roseolus	Antioxidant activity	*in vitro*	(Gursoy et al., 2010) (Kıvrık et al., 2022)
Russula chloroides	Antioxidant and antimicrobial activities	*in vitro*	(Kostić et al., 2020)
Russula delica	Antioxidant activity	*in vitro*	(Gursoy et al., 2010) (Kalogeropoulos et al., 2013)
Schizophyllum commune	Antioxidative activity, α-amylase inhibitory activity	*in vitro*	(Çayan et al., 2021) (Klaus et al., 2011)
	Ethanolic extract had anti-fatigue effects on mice (morusin is most effective)	*in vivo*	(Chen et al., 2024)
	β-Glucan (from *S. commune* (TBG-136)) has shown positive effects on human gut health (increase in beneficial bacteria, improvement in bowel movement frequency, colonic transit time)	Human intervention trial	(Jang et al., 2023)
	β-Glucan (from *S. commune*) protective effects against obesity, diabetes, inflammatory bowel disease (IBD) and constipation in mice	*in vivo*	(Vu et al., 2022)
	β-Glucan (derived from *S. commune)* showed anti-obesity properties in mice	*in vivo*	(Muthuramalingam et al., 2020)
	Anti-biofilm activity and antimicrobial activity	*in vitro*	(Sharma et al., 2024)
	Schizophyllan extracts improve health of cancer patients	Human intervention trial	(Fujimoto et al., 1983)
Suillellus luridus	Polysaccharides showed antihyperglycaemic, antihyperlipidaemic and protective effects in diabetic mice	*in vivo*	(Zhang et al., 2018)
	Antioxidant activity, anticancer (against MCF7, HepG2, NCI-H460 cell lines) and anti-inflammatory effects	*in vitro*	(Souilem et al., 2017) (Kalogeropoulos et al., 2013)
Suillus bovinus	Chitosan (produced from chitin) films show a concentration-dependent effect on cancerous hepatoma (MH-22A) and non-cancerous ovary (CHO), necrosis and apoptosis-like processes	*in vitro*	(Oberemko et al., 2019)
Suillus granulatus	Tetraprenylphenol extracts showed antimicrobial activity against a range of bacterial strains including *E. coli, Micrococcus luteus* and *Aeromonas hydrophyla*	*in vitro*	(Tringali et al., 1989b)
	Suillin extract showed anticancer (cytotoxicity against KB cells (human nasopharyngeal carcinoma), P-388 cells (murine leukemia), NSCLC-N6 (human bronchopulmonary carcinoma)) and antitumor activity (murine model of ascitic P-388 leukemia)	*in vitro*	(Tringali et al., 1989a)
	Extracted heteropolysaccharide showed immunostimulatory activity against macrophages	*in vitro*	(Gao et al., 2022)
	Antioxidative and lymphocyte proliferation activity	*in vitro*	(Zhou et al., 2016b)
Tricholoma columbetta	Antifungal activity	*in vitro*	(Smolskaitė et al., 2015)
Tricholoma ustaloides	Saponaceolides may have anti-carcinogenic properties	*in vitro*	(Gilardoni et al., 2023b)
Volvariella volvacea	Anticancer and thrombolytic activity, tyrosinase and α-glucosidase inhibition	*in vitro*	(Sharif et al., 2018)
	Antioxidant activity	*in vitro*	(Zhang et al., 2008)

β-carotene/linoleic acid assays, as well as the anti-carcinogenic properties. Further research focused on the effects of polysaccharide extracts on cells, animals, and humans. Two human intervention trials examined the impact of β-glucan derived from *S. commune* on gastric cancer and intestinal health and showed that the extracted polysaccharides had positive effects on gut microbiome, bowel movement and life quality (Fujimoto et al., 1983; Jang et al., 2023).

The results highlight that the listed mushrooms have antioxidant, anti-carcinogenic, anti-inflammatory, antimicrobial, neuroprotective, immunomodulatory and anti-diabetic effects, depending on the species and their bioactive compounds.

Toxicological aspects of selected saline mushrooms

There are several toxicological aspects to consider when looking at

mushrooms. As well as whether they contain any toxins, the accumulation of heavy metals and radioactive elements also needs to be taken into account. When assessing the toxicity of fungi, it is essential to first differentiate between those that produce mycotoxins and those that are poisonous. Bennett and Klich (2003) define mycotoxins as "toxins produced by microfungi" (Bennett and Klich, 2003), which are mostly secondary metabolites produced by microfungi that often grow on crops. Examples include aflatoxins and ergot alkaloids. On the other hand, mushroom poisons are toxins and mostly secondary metabolites produced by macrofungi that are ingested intentionally or accidentally. These toxins have different levels of toxicity and can be fatal; for example, the highly poisonous amatoxins are found in species of *Amanita, Galerina* and *Lepiota* (Govorushko et al., 2019b). More than 70 saline mushrooms, which are either inedible or of unknown edibility have been described in literature (Supplementary Tables S1 and S2). Examples include *Leucopaxillus amarus, Agaricus moelleri,* and *Inocybe rimosa* (Govorushko et al., 2019b; Ruiz-González et al., 2023).

Heavy metals such as mercury, arsenic, lead, and cadmium are particularly dangerous to human health. In addition to being acutely toxic, they are carcinogenic and act as metabolic disruptors. Since mushrooms absorb and accumulate heavy metals, it is crucial to monitor their levels if they are used as a food source (Širić et al., 2016). The maximum values set by the European Commission are for lead at 0.3 and 0.8 mg kg^{-1} for cultivated (*A. bisporus, P. ostreatus* and *L. edodes*) and wild fungi, respectively, and for cadmium at 0.05, 0.15 and 0.5 mg kg^{-1} for cultivated fungi (except *P. ostreatus* and *L. edodes*); *P. ostreatus* and *L. edodes*; and wild fungi, respectively (European Commission, 2023). The European Food Safety Authority (EFSA) has stated that the tolerable weekly intake (TWI) of 4 µg kg^{-1} bw (body weight) of inorganic mercury and methylmercury is 1.3 µg kg^{-1} bw (European Food Safety Authority, 2004). However, maximum levels for many foods (including individual and overall mushrooms) have not yet been set due to ongoing monitoring and risk assessment by the EFSA. For arsenic, the reference point is 0.06 µg iAs kg^{-1} bw per day of inorganic arsenic (iAs) (Schrenk et al., 2024). Maximum levels for arsenic in a wide range of food products (including mushrooms) have not yet been set due to variability in the toxicity of different arsenic species, the complexity of exposure assessment, and scientific uncertainty. Considering lead, all saline mushroom species listed in Table 6 except three (*A. mellea, S. luridus* and *H. repandum*) exceed the maximum level. The same applies to cadmium: all species except *H. repandum* exceeds the maximum level. It is more difficult to say this for mercury and arsenic, since there are no maximum levels, only tolerable intakes, which are not specified for the food. Like for arsenic, the toxicity of mercury depends on its form and exhibit different toxicological effects. Mercury exists as metallic, organic and inorganic mercury. Methylmercury and inorganic mercury are of toxicological relevance related to food. Methylmercury is considered of higher toxicological potential than inorganic mercury since its easier uptake in the human body (European Food Safety Authority, 2004). Both species can be found in mushrooms (López et al., 2025). Inorganic arsenic is highly toxic to the human body, while organic arsenic is less toxic. Many species of mushrooms contain organic arsenic in the form of arsenobetaine (AsB). Although AsB is non-toxic, a recent study shows that it can be converted into the toxic inorganic arsenic form As(V)

Table 6
The heavy metal content of the selected saline mushroom species in category E1 is shown in Table 1.

	Mercury [mg kg^{-1} DW]		Arsenic [mg kg^{-1} DW]		Lead [mg kg^{-1} DW]		Cadmium [mg kg^{-1} DW]	
Amanita rubescens	0.1 - 11	(Demková et al., 2025)	1.1	(Rasalanavho et al., 2019)	0.79 - 1.7	(Petkovšek and Pokorny, 2013)	1.3 - 6	(Petkovšek and Pokorny, 2013) (Rasalanavho et al., 2019)
Armillaria mellea					0.49 – 0.79	(Petkovšek and Pokorny, 2013) (Širić et al., 2016)	12.5	(Petkovšek and Pokorny, 2013)
Bovistella utriformis					3.91	(Petkovšek and Pokorny, 2013)	4.51	(Petkovšek and Pokorny, 2013)
Cantharellus cibarius					0.99	(Petkovšek and Pokorny, 2013)	1.25	(Petkovšek and Pokorny, 2013)
Chlorophyllum rhacodes					2.24	(Petkovšek and Pokorny, 2013)	17	(Petkovšek and Pokorny, 2013)
Clitocybe nebularis	1.08	(Širić et al., 2016)			1.39 - 1.52	(Petkovšek and Pokorny, 2013) (Širić et al., 2016)	1.43 - 4.73	(Petkovšek and Pokorny, 2013) (Širić et al., 2016)
Collybia nuda					2.67	(Petkovšek and Pokorny, 2013)	1.77	(Petkovšek and Pokorny, 2013)
Hydnum repandum					0.46	(Petkovšek and Pokorny, 2013)	0.33	(Petkovšek and Pokorny, 2013)
Laccaria laccata	0.21	(Kula et al., 2011)	14.1 - 143	(Zhang et al., 2015)	9.15	(Kula et al., 2011)	5.28	(Kula et al., 2011)
Lycoperdon perlatum	2.4	(Bergin et al., 2021)	0.57 - 4.5	(Falandysz et al., 2012)	5.97	(Petkovšek and Pokorny, 2013)	1.86	(Petkovšek and Pokorny, 2013)
Bovistella utriformis					3.91	(Petkovšek and Pokorny, 2013)	4.51	(Petkovšek and Pokorny, 2013)
Macrolepiota procera			0.5 - 1.8	(Stefanović et al., 2016)	1.67 - 2.58	(Petkovšek and Pokorny, 2013) (Širić et al., 2016)	2.3 - 6.68	(Petkovšek and Pokorny, 2013) (Širić et al., 2016)
Marasmius oreades	0.28	(Bergin et al., 2021)						
Pleurotus ostreatus			1.4	(Rasalanavho et al., 2019)	2	(Rasalanavho et al., 2019)	2	(Rasalanavho et al., 2019)
Rhizopogon roseolus	0.3	(Kula et al., 2011)			4.55	(Kula et al., 2011)	1.67	(Kula et al., 2011)
Russula cyanoxantha					1.17	(Petkovšek and Pokorny, 2013)	2.38	(Petkovšek and Pokorny, 2013)
Russula delica	0.54	(Kula et al., 2011)			1.42	(Kula et al., 2011)	1.77	(Kula et al., 2011)
Suillellus luridus					0.14	(Petkovšek and Pokorny, 2013)	1.15	(Petkovšek and Pokorny, 2013)
Suillus bovinus	≤ 1.0	(Saba et al., 2016)			0.75	(Petkovšek and Pokorny, 2013)	1.36	(Petkovšek and Pokorny, 2013)
Suillus granulatus					0.41	(Petkovšek and Pokorny, 2013)	3.46	(Petkovšek and Pokorny, 2013) (Rasalanavho et al., 2019)
Suillus luteus			0.57	(Rasalanavho et al., 2019)	0.55 – 1.2	(Petkovšek and Pokorny, 2013) (Rasalanavho et al., 2019)	0.69 - 1	(Petkovšek and Pokorny, 2013)
Termitomyces umkowaan			2	(Rasalanavho et al., 2019)	2	(Rasalanavho et al., 2019)	0.4	(Rasalanavho et al., 2019)
Xerocomellus chrysenteron	0.01 - 2.61	(Demková et al., 2021)	0.83	(Šíma et al., 2019)	0.09	(Šíma et al., 2019)	0.07	(Šíma et al., 2019)

(Zhang et al., 2023). Nearing et al. (2014) stated that both organic arsenic and inorganic arsenic can be found in mushrooms, with higher levels found in wild mushrooms than cultivated ones. For example, levels of up to 16.9 μg/kg could be found in wild *C. cibarius* (Schrenk et al., 2024).

The heavy metal content depends on the species of mushroom, as well as its morphology and the environment (Nearing et al., 2014). The heavy metal content and distribution in mushrooms can be influenced by factors such as tree richness, soil pH and C/N ratio (Stojek et al., 2024). Especially, anthropogenic contamination of the environment influence the heavy metal content in mushrooms. For example, urban pollution from inorganic compounds or silver mining residues can lead to increased levels of heavy metals (Svoboda et al., 2006; Zsigmond et al., 2023). When grown on cultured media, the mushrooms *Bacillus badius* and *C. cibarius* were found to contain lower levels of toxic elements (Reczyński et al., 2013), making controlled cultivation a good alternative for areas with contaminated soils. Besides heavy metals, as well radioactive elements are a toxicological issue regarding the consumption of mushrooms. Fungi lack the ability to differentiate between the uptake of radio cesium (^{137}Cs) and potassium (Vinichuk et al., 2010). A more recent study suggests that there is no correlation between cesium and potassium uptake (Ogo et al., 2017). Radio cesium is still found in considerable amounts in soil across Europe, particularly in contaminated areas such as Chernobyl. Consequently, it can accumulate in mushrooms at a higher concentration than in other foods (Falandysz et al., 2022).

Discussion

The aim of this review was to give a comprehensive overview of edible mushrooms for saline cultivation, here called saline mushrooms, and evaluate their potential as a future food. Eighty-six saline mushroom species were identified, and their nutritional and toxicological properties were evaluated. As there are few studies on mushrooms and salinity, it is important to establish how salinity could affect mushrooms and where the research gaps lie. In order to compare saline mushrooms with those cultivated without salinity, we must distinguish between saline and classical mushroom cultivation.

Mushroom cultivation and salinity tolerance

The most commonly cultivated species of mushroom in classical cultivation are *Agaricus bisporus* (button mushroom), *Pleurotus* species (oyster mushroom), *Lentinula edodes* (shiitake), *Auricularia* species (wood ear mushroom), *Flammulina velutipes* (Enoki), and *Volvariella* species (paddy straw mushroom) (Grimm and Wösten, 2018; Suwannarach et al., 2022). These mushrooms are cultivated on lignocellulosic material enriched with nutrients. The material chosen depends on whether the mushroom is a primary, secondary or tertiary decomposer, so that it can grow directly on plant material, compost or soil, respectively. The most commonly used materials originate from agri-industrial by-products, such as sawdust, wheat straw, rice straw, barley straw and oak straw (Suwannarach et al., 2022). However, depending on the substrate, they can introduce heavy metals or other contaminants from fertilizers, pesticides, wastewater or manure (Ab Rhaman et al., 2021). Therefore, the substrates must be selected according to the species of fungi and evaluated for their toxicological properties.

In addition to the existing substrates, alternative residual and waste streams can be exploited for the saline mushroom cultivation, which is improving circular economy and sustainable cultivation. For instance, the *Pleurotus* species has been cultivated on reed (*Phragmites australis*) from saline wetlands (Li et al., 2023a). Furthermore, the reed-mushroom leftovers after harvesting the fruiting bodies were used to fertilize saline wetland soil by decreasing its pH and increasing its organic matter content (Li et al., 2023b). Further potential substrates for growing saline mushrooms could be waste products from the production of salted foods, such as pickles, cheese or fish. Other possibilities include salinized soils or residues from saline agriculture, e.g. halophytes (salt plants) residues. It is vital to investigate the accumulation of toxins, contaminants and heavy metals, particularly in residues from industrial production.

A study of *P. tuber-regium* investigated the impact of several salts and concentrations on mycelium growth in sawdust saturated with salt solutions (Ayodele and Ojoghoro, 2007). The results showed that the higher the sodium chloride concentration, the longer it took for the spawn to colonize the entire substrate. At a concentration of 15 % NaCl, no mycelium grew anymore. They also demonstrated that different salts have different effects on fungal growth. They discovered that chloride ions associated with sodium, potassium and magnesium led to greater growth reduction than sulphate salts containing the same cations. This suggests that chloride ions may play a more significant role in salt toxicity.

When it comes to choosing the right substrate for saline mushroom cultivation, knowing the salt tolerance of the species is of great importance. Only seven of the 86 species have had their salinity tolerance determined by cultivation on saline media; examples include *S. luridus, R. roseolus* or *S. granulatus* (see Table 1, S1; (Tang et al., 2009; Mousa, 2020; Nakano et al., 2022). These species can therefore be classified into salinity ranges according to their salt tolerance. This needs to be done for all potential saline mushrooms to confirm their tolerance and classify them accordingly. Further research should focus on the mechanisms behind salinity tolerance in fungi and whether it is species-specific.

When it comes to sustainability, mushroom farming is more efficient than producing animal-based food. For example, 10 m^2 of land is needed to produce 1 kg of mushrooms, whereas 27 m^2 of land is needed to produce 1 kg of beef (Vu et al., 2018). Mushroom production also uses less water and results in lower GHG emissions (Da Lee et al., 2025). In sustainable mushroom cultivation, using a sustainable substrate is important, as is considering the fungal waste, such as spent mushroom substrate. This can be used for composting, cultivating other mushrooms, producing animal feed and materials, and extracting compounds or enzymes for biotechnology (Grimm and Wösten, 2018).

In summary, saline mushroom cultivation has the potential to exploit alternative cultivation materials from residual and waste streams, thereby improving sustainability of the agri-food-system. However, further research is needed on salinity tolerance and substrate suitability of mushrooms.

Edibility and nutritional properties

In terms of edibility, the saline mushrooms in categories E2 and E3 should undergo further testing. This could be achieved by screening for toxic secondary metabolites. Further advanced processing methods, such as fermentation, could be investigated to improve the properties of mushrooms that are currently inedible due to their texture, taste or odor. The use of salt-tolerant mushrooms as edible mushrooms requires not only consideration of their edibility but also compliance with the legal frameworks. When considering the edibility of saline mushrooms, both the biological edibility and the regulatory framework should be taken into account. There are no specific legal regulations for saline fungi, as these have not yet been categorized as a separate food group. The generally applicable regulations for edible fungi apply. On an international scale, the Codex Alimentarius (CXS 38–1981) regulates all edible fungi, whether fresh or processed (Joint FAO/WHO, 1981). It defines quality criteria such as water content or permitted levels of impurities, labelling, hygiene practice and packaging. Further regulations exist at a national level, for example in the US, Canada, Japan and the EU. The EU's regulations are highly diverse, providing a good example of how complex these regulations can be. In the EU, edibility is regulated by the General Food Law and the Novel Foods Regulations. When it comes to fungi, it is important to distinguish between fruiting bodies, mycelia, and mushroom products (Molitorisová et al., 2025). Fruiting bodies are considered food under Regulation (EC) No 178/2002 (General Food

Law), but mycelium and mushroom products are not. Therefore, the fruiting body of a fungal species can be considered non-novel food and consumed, while the mycelium is classified as novel food. Of the identified species, few are listed in the novel foods catalogue. For instance, the fruiting body and β-glucan of *Pleurotus ostreatus* are not considered novel foods, as these were already consumed before 1997, and thus be marketed as food. However, mycelium and dehydrated mycelium powder are considered novel foods (European Commission, 2025). For *Pleurotus pulmonarius*, only the mycelium biomass is listed and is classified as novel food. For *Ganoderma lucidum*, the fruiting bodies and aqueous extract powder are not classified as novel foods, but the dehydrated mycelium powder is. *Volvariella volvacea* is not classified as novel food, whereas *Trametes versicolor* is. The fruiting bodies of *Suillus luteus* are not classified as novel foods. All other species are classified as novel foods if they were not consumed in significant amounts in the EU before 1997. Individual classification would be needed for each species.

The nutritional profile of saline mushrooms is most likely influenced by salinity. However, studies investigating the impact of salinity on the nutritional properties of saline mushrooms are scarce. Nevertheless, the identified species exhibit comparable nutritional properties to those of common mushroom species. For example, *Pleurotus* spp. are included. It is only possible to estimate how salinity could influence nutritional properties. As there are already studies on the influence of salinity on microfungi, we might be able to draw some inspiration from them. For example, they show that ergosterol is connected to resistance against environmental stresses (Eliaš et al., 2024). In particular, it has been shown to improve the mechanical resistance of the plasma membrane to osmotic stress in *Saccharomyces cerevisiae* during salt stress (Kodedová and Sychrová, 2015). The role of ergosterol in salt tolerance has not yet been investigated for macrofungi. However, it has been demonstrated that the ergostane-type sterols found in *Russula cyanoxantha* are similar to those found in marine fungi. Consequently, it has been proposed that they possess identical biosynthetic pathways (Gao et al., 2001). These findings could suggest that ergosterol is also involved in the salt tolerance of halophilic macrofungi, and further research is needed to confirm this. Furthermore, reactive oxygen species (ROS) are formed during salinity stress, which influences the accumulation of antioxidant compounds such as phenolic compounds, carotenoids and tocopherols due to their function as ROS scavenging molecules. Further research is needed to confirm the impact of salinity on the level of antioxidants and the antioxidant capacity of mushrooms grown in saline conditions. Furthermore, a study by Pyeon et al. (2022) study the influence of different NaCl concentrations in mycelia growth on the gene expression. They found out that there is an increase in gene expression of a gene that is responsible for the activity of an NADPH dependent aldo-keto reductase and an α-1,4-glucan phosphorylase. The latter is responsible for the reversible degradation of polysaccharides and maintaining cellular glucose homeostasis. As glucose is an osmolyte, it helps the mushrooms maintain their osmolar balance and cope with ionic stress caused by an excess of sodium and chloride ions (Burg and Ferraris, 2008).

In summary, mushrooms cultivated in saline conditions have great potential to become an important source of protein, carbohydrates and bioactive compounds, and a nutritious addition to the human diet.

Toxicological properties

Studies on halophilic macrofungi are very limited when toxicological aspects are considered. However, as the accumulation of toxic compounds is greatly affected by environmental factors, it is highly probable that salt stress influences the presence of these compounds. For example *A. phalloides*, showed to have different amount of amatoxin and phallotoxin depending on the soil characteristics (Enjalbert et al., 1999). It is possible that toxins, which are primarily secondary metabolites, increase in response to salt exposure, rendering these mushrooms inedible. Further research in this area is needed. In classical mushroom cultivation, heavy metal accumulation depends heavily on the species (Table 6) and the use of substrates. Heavy metals such as cadmium, arsenic, zinc and lead can be introduced and accumulated by fungi depending on the substrate (Ab Rhaman et al., 2021). These values are comparable to those found in plants; however, some mushroom species may accumulate heavy metals at higher levels (Ab Rhaman et al., 2021).

No studies have yet been conducted on the accumulation of heavy metals in saline mushroom cultivation. However, a possible link could be drawn with halophytic plants. Some of these plants can accumulate and compartmentalize salt in their vacuoles; they also accumulate heavy metals in this way. This raises the question of whether halophilic fungi also have the ability to accumulate heavy metals in relation to their salt tolerance. Halophilic microfungi also demonstrate resistance to high levels of heavy metals (Yovchevska et al., 2025). Some of the mechanisms that confer salt tolerance also help with resistance to heavy metals. Firstly, compartmentalization and enhanced transporters help to counteract the toxic effects of heavy metals in the cell. Salt-dependent transporters, for example, are also involved in accumulating heavy metals (Gajewska et al., 2022; Gostinčar and Gunde-Cimerman, 2023). Secondly, a thickened cell wall and protective pigmentation help with osmotic stress and uptake. For example, a higher melanin content stabilizes the cell wall against changes in turgor pressure (Gostinčar and Gunde-Cimerman, 2023). Furthermore, melanin can chelate the metals and absorb them at the cell wall (Gajewska et al., 2022). If they are exposed to an increased heavy metal content, this can lead to higher levels of heavy metals in the saline mushrooms. However, it may also influence the bioavailability of the metals. Furthermore, it was demonstrated that there may be an interaction between salt stress and the high-metal signaling pathways. In particular, the HOG (high osmolarity glycerol) pathway may be connected to the high metal signaling pathway (Yovchevska et al., 2025). Finally, some fungi can excrete salt and heavy metals in the form of guttation droplets via their aerial hyphae (Pereira et al., 2012). Further research could focus on investigating the excretion of salt and heavy metals in guttation droplets. Once again, research has focused primarily on microfungi and can likely not be transferred one-to-one to macrofungi. Therefore, it is crucial that future research focus on the relationship between salinity and heavy metal accumulation in macrofungi.

In summary, the content of toxins and heavy metals require precise monitoring and further research to ensure the quality and safety of mushrooms cultivated in saline conditions. However, controlled cultivation has the major advantage of enabling substrates to be used consistently and in a controlled manner, thereby minimizing their influence on toxin biosynthesis and heavy metal accumulation.

Conclusion and future perspectives

The aim of this review was to identify mushrooms for saline cultivation and evaluate their nutritional and toxicological properties. Eighty-six species of saline mushrooms were identified to be a potential food source. Several studies demonstrated their richness in proteins, in bioactive compounds and their potential bioactive properties. Including several species of mushroom improves our diet, thus improving health by diversifying the gut microbiome and increasing nutrient uptake. Increasing the diversity of species in food production will also boost biodiversity, which aligns with SDG 15 (Life on Land). Furthermore, considering a balanced diet, SDG 3 (good health) can be promoted by the high concentration of bioactive compounds, such as phenolic compounds, polysaccharides and vitamins, which reduce the risk of non-communicable diseases (NCDs). In terms of planetary health, the reduced use of land and water in saline mushroom farming, as well as lower greenhouse gas (GHG) emissions compared to animal-based foods, will help to prevent the further deterioration of the planet's boundaries. Compared to plant indoor farms, mushrooms require little or no light, which drastically reduces indoor farm energy consumption. Additionally, mushroom production is more resilient. They can easily be

produced indoors and are therefore resilient to extreme weather events, which are increasing due to climate change. Their easy and fast indoor cultivation also makes them more resilient to other crises, such as war or trade disruptions. This contributes to ensuring food security and improving SDG2 (zero hunger).

This extensive list highlights their potential value for human nutrition and the need for further research. Thus, essential research gaps were identified and research questions selected: What is the salinity tolerance of the identified species? What mechanisms lead to salinity tolerance in mushrooms, and are these mechanisms species-specific? How does salinity influence the nutritional properties of food? Can salinity be used to stimulate the production of beneficial compounds? What effect is salinity having on the accumulation of heavy metals and toxic metabolites? Is there a link between salinity tolerance and the accumulation of heavy metals? Which substrates can be used for saline mushroom cultivation? What is the toxicological risk of these substrates? How do these substrates influence nutritional properties? How can waste management be optimized to eliminate the production of saline waste? This review demonstrates the high potential of saline mushrooms to become a future food, opening a new field of research that requires extensive investigation.

Ethical statement - studies in humans and animals

Not available.

CRediT authorship contribution statement

Maria Fitzner-van Bömmel: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Susanne Baldermann:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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Data availability

Data will be made available on request.

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