Colegio de Postgraduados

Antibacterial activity of polysaccharides from the fruiting bodies of *Boletus edulis* and *Lactarius indigo*

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ABSTRACT

Objective: This study aimed to evaluate the antibacterial activity of aqueous and alkaline polysaccharide fractions extracted from wild fruiting bodies of *Boletus edulis* and *Lactarius indigo* from central Mexico.

Design/methodology/approach: Polysaccharides were obtained and separated into aqueous (FAq) and alkaline (FAk) fractions, characterized by Fourier transform infrared spectroscopy (FTIR), and tested at concentrations of 500, 250, 125, and 62.5 μg mL^{-1} using the broth dilution method against *Staphylococcus aureus*, *Escherichia coli*, *Enterococcus faecalis*, and *Streptococcus mutans*.

Results: Four polysaccharide fractions were obtained (FAqBe, FAkBe, FAqLi, and FAkLi). All fractions exhibited antibacterial activity, with the highest inhibition (up to 97.6%) observed against *S. aureus* at 500 μg mL^{-1} of FAkBe. A significant concentration-dependent inhibitory effect was detected.

Limitations on study/implications: However, further studies are required to elucidate the molecular mechanisms involved and to evaluate *in vivo* efficacy.

Findings/conclusions: These findings suggest that polysaccharides from wild edible mushrooms represent a promising source of bioactive compounds with antibacterial potential.

Keywords: Antibacterial activity, Aqueous and alkaline fractions, Bioactive polysaccharides, Functional foods, Wild edible mushrooms.

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INTRODUCTION

Edible mushrooms are valued as healthy foods with high nutritional content (Reis *et al.*, 2017). They contain a high concentration of carbohydrates and proteins, in addition to a considerable concentration of vitamins, minerals and fiber, with low levels of sodium and

unsaturated fats (Stamets, 2011). Edible mushrooms are also used in traditional medicine and are attributed with healing and therapeutic value (Guzmán, 2008), presenting immunomodulatory, anticancer and antibacterial properties (Cano-Estrada and Romero-Bautista, 2016).

Traditional knowledge has served as the basis for demonstrating the bioactivity of edible mushrooms against chronic degenerative diseases such as cancer, or cardiovascular, neurodegenerative and immunomodular diseases (Roncero-Ramos and Delgado-Andrade, 2017), as well as for the development of products for the food (Pizarro *et al.*, 2014; Reis *et al.*, 2017), pharmaceutical and cosmetic industries (Khan *et al.*, 2018).

Various studies have shown that the bioactivity of fungi is related to compounds present in their structure (Sari *et al.*, 2017; Muszyńska *et al.*, 2018). Polysaccharides are the most abundant structural compounds found in the cell walls of fungi (Arango and Nieto, 2013; Rathore *et al.*, 2017; Khan *et al.*, 2018). At structural level, polysaccharides can be found in the form of homopolysaccharides, heteropolysaccharides and glycoproteins (Donot *et al.*, 2012), and they have shown great potential as anticancer, antioxidant and antibacterial agents (Wasser, 2002; Chen *et al.*, 2012).

The polysaccharides present in basidiomycetes are composed of monosaccharides units linked by glycosidic bonds (Pizarro *et al.*, 2014). The bioactivity of polysaccharides is largely attributed to their structural variability (Synytsya and Novak, 2014), molecular mass, chain length (Wasser, 2002), solubility properties (Xiao *et al.*, 2004), branching frequency (Miyazaki *et al.*, 1979) and shaping in solution (Zhang *et al.*, 2004; Khan *et al.*, 2018).

It is important to note that, despite the great importance of edible mushrooms as functional foods (Wasser, 2002; Reis *et al.*, 2017), few studies have addressed wild edible mushrooms as a source of nutraceuticals (Arango and Nieto, 2013), particularly in traditionally valued yet understudied species such as *Boletus edulis* and *Lactarius indigo*. In addition to the nutritional, medicinal and economic value of *B. edulis* (Cano-Estrada and Romero-Bautista, 2016), studies have shown that some acetone and methanol extracts obtained from fruiting bodies of *B. edulis* exert a strong antimicrobial effect against bacteria such as *Escherichia coli* and *Staphylococcus aureus* (Kosanić *et al.*, 2012), as well as antioxidant activity (Tsai *et al.*, 2007) and antiproliferative and antitumor effects (Lemieszek *et al.*, 2013). *Lactarius indigo* is a species of both nutritional and pharmaceutical importance (Cano-Estrada and Romero-Bautista, 2016), since aqueous and organic extracts of its fruiting bodies have shown antibacterial activity against *Escherichia coli*, *Pseudomonas aeruginosa*, *Enterobacter cloacae*, *Staphylococcus aureus* and *Salmonella enterica*, and antiproliferative activity against MCF7 cells (Ochoa-Zarzosa *et al.*, 2011), in addition to antitumor and anti-inflammatory effects (Cano-Estrada and Romero-Bautista, 2016). Moreover, various studies describe different antibacterial mechanisms, including the alteration and degradation of bacterial cell walls and cytoplasmic membranes (Cheng *et al.*, 2024; Liang *et al.*, 2024), as well as the penetration of polysaccharides into gram-positive bacteria due to the absence of an outer membrane composed of lipopolysaccharides or a phospholipid layer (Norhisham *et al.*, 2025). The aim of this study was to evaluate the antibacterial activity of an aqueous and alkaline fraction of polysaccharides from the fruiting bodies of wild *B. edulis* and *L. indigo* of central Mexico.

MATERIALS AND METHODS

Biological material

The study utilized the fruiting bodies of wild *B. edulis* and *L. indigo* collected in the Área de Protección de Flora y Fauna Nevado de Toluca (APFFNT), Mexico.

Obtaining biomass

The collected specimens (*Boletus edulis* 2000 g; *Lactarius indigo* 1600 g) were characterized and taxonomically identified according to Franco Maass *et al.* (2012). They were then oven-dried at 60 °C for 48 h in order to calculate the water content (Equation 1), then ground to obtain a powder, which was used for the extraction of polysaccharides.

$$\%\, of\ water = \frac{\left(fresh\, weight\, of\ biomass\left(g\right) - dry\, weight\, of\ biomass\left(g\right)\right)}{\left(fresh\, weight\, of\ biomass\left(g\right)\right)} \times 100 \qquad (1)$$

Extraction of crude polysaccharides

Biomass macerate: The dry biomass of the fruiting bodies of *B. edulis* (BFBe 103.87 g) and *L. indigo* (BFLi 142.37 g) was placed individually in 10 volumes of 70% ethanol for 24 h in order to eliminate apolar and low molecular weight compounds. This procedure was performed twice (Carbonero *et al.*, 2006). The biomass was subsequently recovered by filtering through filter paper of coarse porosity, discarding the ethanol.

Aqueous extraction: The biomass of the fruiting bodies recovered from the previous process was placed in 10 volumes of distilled water at 121 °C and 15 lbs for 60 min (Klaus *et al.*, 2011). The biomass was then filtered (cellulose filter of pore size 125 μm), obtaining an aqueous extract of crude polysaccharides in the filtrate and leaving the remaining biomass as a residue.

Alkaline extraction: The biomass from the aqueous extraction was recovered and placed in 10 volumes of an aqueous solution of NaOH at 2% (w/v) with 0.1% of $NaBH_4$, and heated at 80 °C for 4 h and subsequently neutralized with acetic acid (Klaus *et al.*, 2011). The resulting alkaline extract (Mizuno *et al.*, 1992) of crude polysaccharides was then filtered through a cellulose filter of pore size 125 μm and the biomass residue discarded.

Purification of polysaccharides

Ethanol precipitation: The aqueous and alkaline extracts of crude polysaccharides were placed individually in three volumes of cold ethanol (Smiderle *et al.*, 2013) in order to precipitate polysaccharides from the complexes of low molecular weight molecules (Carbonero *et al.*, 2006). Finally, the precipitates with polysaccharides corresponding to each extract were recovered.

Freezing-thawing of the precipitates: the precipitates with polysaccharides obtained were frozen and then slowly thawed at room temperature in order to eliminate linear compounds with a lower degree of branching. This process was carried out several times until there was no further formation of precipitate from the supernatant.

The precipitates from this process containing polysaccharides were recovered and centrifuged at 8000 rpm for 15 min at 15 °C (Smiderle *et al.*, 2013). The precipitates obtained from the centrifugation were then filtered through a cellulose acetate membrane of 0.2 μm in pore size. Two fractions of polysaccharides of each species were thus obtained: an aqueous fraction (FAq) and an alkaline fraction (FAk).

Identification of polysaccharides

A sample of each fraction (0.1 g) was oven-dried at 60 °C for 48 h until obtaining crystals, which were analyzed by FTIR under an absorbance range of 4000-400 cm^{-1} using the KBr disk technique (Mizuno *et al.*, 1992; Klaus *et al.*, 2011) to identify the vibrational mode of the characteristic bonds of polysaccharides (Alzorqi *et al.*, 2017). In addition, the regions associated with sugars, the anomeric region and the region associated with proteins were analyzed, corresponding to 3200, 2920, 1640, 1160, 1070, 1040, 970 and 890 cm^{-1} (Synytsya and Novak, 2014).

Antibacterial activity

The antibacterial activity test was carried out by dilution in broth according to the Clinical and Laboratory Standards Institute (CLSI, 2018). For this purpose, four strains of bacteria from the culture collection of the Laboratorio de Bioquímica de la Facultad de Odontología of the Universidad Nacional Autónoma de México (UNAM) were used: *Staphylococcus aureus*, *Escherichia coli*, *Enterococcus faecalis* and *Streptococcus mutans*. These were reactivated through inoculation onto sterile Muller-Hinton agar (38 g L^{-1}) and incubated at 38 °C for 24 h. Bacterial cultures were diluted in saline solutions to make a bacterial suspension according to the McFarland 0.5 standard. In a 96-well plate, a volume of 200 μL of sterile Muller-Hinton broth was added per well and inoculated with 5 μL of the bacterial suspension (approximately 5×10^5 CFU mL^{-1}). Moreover, a stock of each fraction was prepared and added to each well, with final concentrations of: 500, 250, 125 and 62.5 μg mL^{-1} of polysaccharides. Sterile culture broth was used as a positive control, culture broth inoculated with bacteria as a negative control and sterile culture broth with different concentrations of polysaccharides was used as a blank. The plate was incubated at 38 °C for 24 h in an orbital shaker at 200 rpm. The two fractions of both species were applied in four concentrations to the four bacteria, with each treatment performed in quadruplicate in the wells (4 fractions × 4 concentrations × 4 bacteria × 4 repetitions in wells). Following incubation, the plate was analyzed in a plate reader in absorbance mode at 630 nm in order to determine the percentage viability of the bacterial inoculum compared to the untreated inoculum (Equation 2).

$$\%\,inhibition = \frac{\left(Treatment - Blank\right)}{\left(Negative\ control - Positive\ control\right)} \times 100 \qquad (2)$$

where: the treatment was culture broth inoculated with bacteria and polysaccharides at different concentrations, the blank was culture broth and polysaccharides at different

concentrations, the negative control was medium inoculated with bacteria and the positive control was sterile culture broth.

Data collection and analysis

The data were collected and restructured into a long format, with each bacterial strain, treatment, and dosage combination treated as separate observations. The variable "dosage" was converted into a factor to perform categorical analysis. The dataset was structured to include the factors treatment, dose, and bacteria.

An analysis of variance (ANOVA) was performed to compare the inhibitory effects of the treatments, dosages, and bacterial strains. A simplified ANOVA model without interaction terms was used to identify the main effects. Tukey's post-hoc test was applied to evaluate pairwise differences between the treatments, dosages, and bacterial strains, with significance set at $p<0.05$. All analyses were conducted using R statistical software.

RESULTS AND DISCUSSION

Obtaining biomass

The fruiting bodies of *B. edulis* Pers Bull collected in *Abies* and *Abies-Pinus* forests at 3100-3500 m agreed with that reported by Franco Maass *et al.* (2012). The fruiting bodies presented a water content of 94.8 %. Macroscopically, they presented crowns of 8-15 cm in diameter, yellow-brown-reddish coloration, a midstipe of 7 to 20 cm in length and white to light brown in color. Microscopically, they presented basidia of 29.3×11 μm and spindle-shaped and smooth basidiospores of 15.6- 4.6 μm. Likewise, the fruiting bodies of *L. indigo* (Schwein.) Fr. collected from *Pinus* forests at 3100-3500 m, agreed with that reported by Franco Maass *et al.* (2012).

They presented a water content of 91.1%. Macroscopically, the crowns were 7.5 cm in diameter, convex and umbilicus when ripe, indigo blue in color with grayish concentric areas and with slightly decurrent separated blades of indigo blue color. The stipe measured 4 cm and was blue and smooth. The basidia measured 5.1×22 μm, with a smooth-nailed shape, are hyaline and tetraesterygmatic, while the basidiospores were oval, measured 5.6×7.3 μm and were hyaline and smooth.

Extraction and purification of polysaccharides

Total polysaccharides extracted from *B. edulis* were equivalent to 16.04 g of polysaccharides per 100 g of dry biomass, of which 12.36 g of polysaccharides per 100 g of dry biomass corresponded to the alkaline fraction (FAkBe) and 3.68 g of polysaccharides per 100 g of dry biomass to the aqueous fraction (FAqBe). Regarding L. indigo, 16.42 g of polysaccharides were obtained per 100 g of dry biomass, and 12.86 g of polysaccharides per 100 g of dry biomass corresponded to the alkaline fraction (FAkLi) and 3.56 g of polysaccharides per 100 g of dry biomass to the aqueous fraction (FAqLi). The alkaline fraction exhibited a higher concentration than the aqueous fraction.

Identification of polysaccharides

The FTIR spectra of the four fractions (Figure 1) show the characteristic vibrational mode of the bonds of polysaccharides (Movasaghi *et al.*, 2008). In the spectra of the fractions of *B. edulis* (FAqBe and FAkBe) (Figure 1A) and of *L. indigo* (FAqLi and FAkLi) (Figure 1B), there is a band at 3200 cm^{-1} corresponding to the vibrational mode of the hydroxyl bond OH, a band at 2920 cm^{-1} corresponding to the saturated CH bond (Šandula *et al.*, 1999) and a signal from 1160 to 1140 cm^{-1} related to the stretching of the C-O-C glycosidic bond, where the signal at 1040 cm^{-1} corresponds to the stretching C-O bond (Münzberg *et al.*, 1995). The characteristic bands of the carbon-glucoside bonds of a polysaccharide corresponding to 1160, 1080, 1040, 970 and 890 cm^{-1} (Alzorqi *et al.*, 2017) were also presented, associated with the sugar region in the range of 1200 cm^{-1} to 950 cm^{-1} and the anomeric region in the range of 950 cm^{-1} to 750 cm^{-1} (Synytsya and Novak, 2014).

The four fractions (Figure 1) present an absorption signal at 1640 cm^{-1}, which is associated with the stretching vibrations of the carbonyl C-O bond of a polysaccharide-protein complex (Alzorqi *et al.*, 2017), The polysaccharides of these fractions of *B. edulis* and *L. indigo* could therefore be protein-coupled.

Antibacterial activity

The different concentrations (500, 250, 125 and 62.5 $\mu g\ mL^{-1}$) of the aqueous and alkaline fractions of both species showed inhibition in the four bacterial strains (*S. mutans*, *S. aureus*, *E. coli* and *E. faecalis*). The analysis of variance (ANOVA) indicated significant main effects of treatment ($p=0.00501$), dose ($p=2.2\times10^{-9}$), and bacteria ($p=1.43\times10^{-7}$) on bacterial inhibition. These results suggest that both the type of treatment and dosage level significantly affect bacterial inhibition, and the response varies depending on the bacterial strain.

The concentrations with the highest percentage of inhibition (Figure 2) in *S. mutans* were of FAqBe at 500 $\mu g\ mL^{-1}$ with 71.2% of inhibition and 250 $\mu g\ mL^{-1}$ with 66.31% of

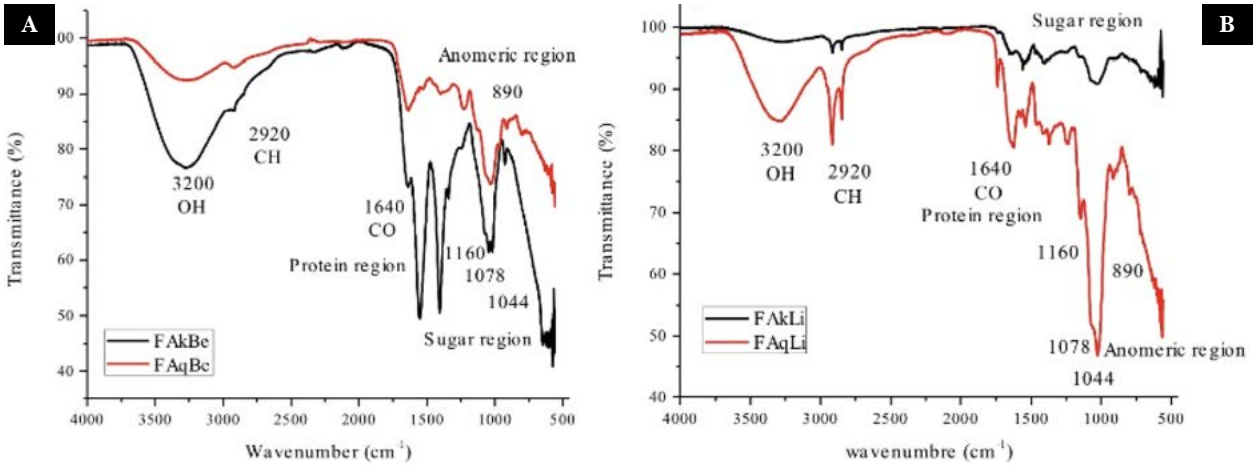

Figure 1. FTIR spectra of polysaccharide fractions obtained from *Boletus edulis* and *Lactarius indigo*: (A) aqueous (FAqBe) and alkaline (FAkBe) fractions of *B. edulis*; (B) aqueous (FAqLi) and alkaline (FAkLi) fractions of *L. indigo*.

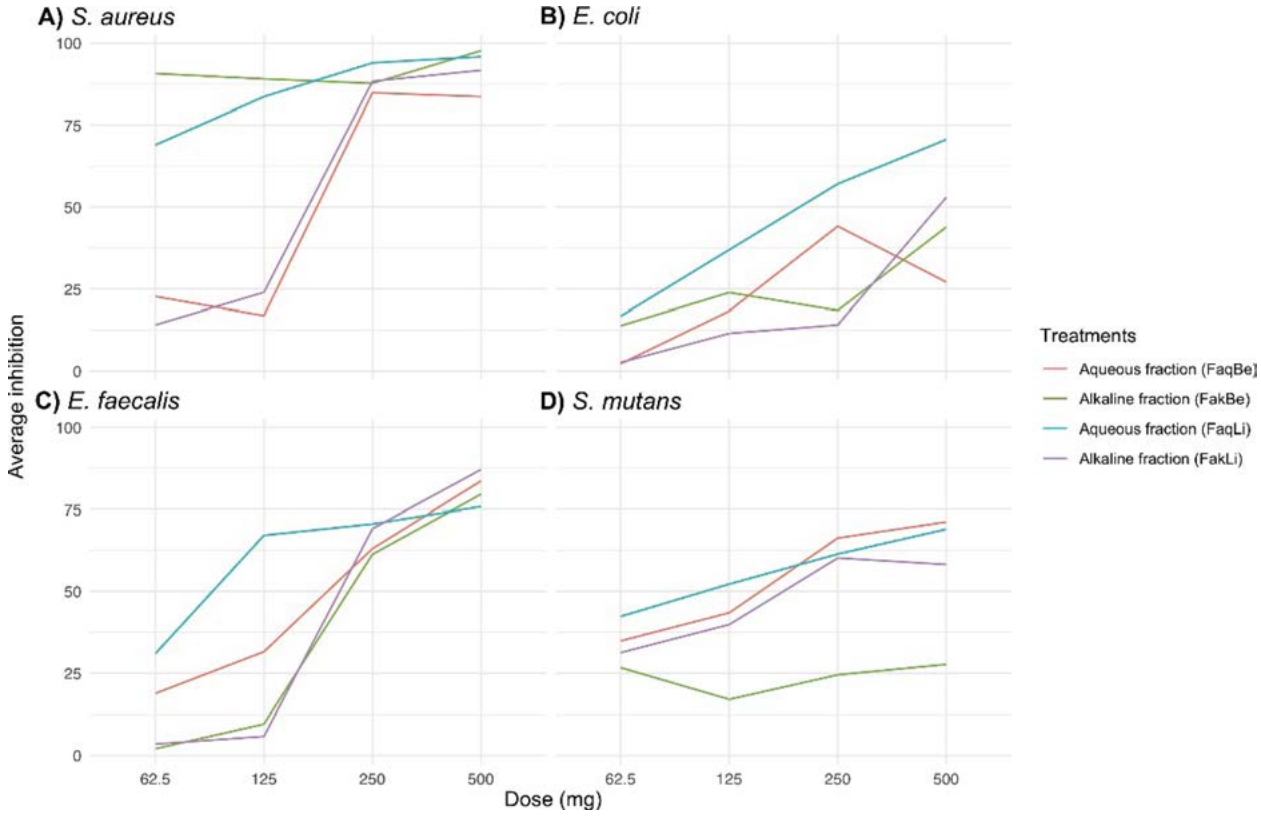

Figure 2. Antibacterial activity of polysaccharide fractions extracted from wild edible mushrooms. (A) Aqueous fraction of *Boletus edulis* (FAqBe), (B) alkaline fraction of *B. edulis* (FAkBe), (C) aqueous fraction of *Lactarius indigo* (FAqLi), and (D) alkaline fraction of *L. indigo* (FAkLi). Inhibition percentage (%) was determined using the broth dilution method at concentrations of 500, 250, 125, and 62.5 μg mL^{-1} against *Staphylococcus aureus*, *Escherichia coli*, *Enterococcus faecalis*, and *Streptococcus mutans*.

inhibition. For *E. coli*, FAkBe at 500 μg mL^{-1} presented 43.91 % of inhibition, and FAqBe at 250 μg mL^{-1} presented 44.15 % of inhibition. In the case of *E. faecalis*, both FAqBe and FAkBe at 500 μg mL^{-1} showed the highest percentages of inhibition, with values of 83.60% and 79.55%, respectively. On the other hand, *S. aureus* reached values of up to 97.64% of inhibition at 500 μg mL^{-1} of FAkBe.

Each fraction exhibited strong antibacterial activity on the four strains (Figure 2). In general, the highest percentage of inhibition of the four fractions was obtained at the highest concentration (500 μg mL^{-1}), approaching the positive control (sterile culture broth), while the lowest percentage of inhibition was at the lowest concentration (62.5 μg mL^{-1}), close to the negative control (bacterial inoculum with culture broth). However, FAqBe and FAkLi showed greater inhibition in *S. mutans* from the lowest concentration (62.5 μg mL^{-1}). Likewise, FAkBe and FAqLi presented greater inhibition on *S. aureus* at all concentrations.

Tukey's *post-hoc* test (Figure 3) revealed several significant pairwise comparisons: FAqLi was significantly more effective than both FAqBe ($p=0.0308$) and FAkBe ($p=0.0315$), particularly for *S. aureus* and *E. faecalis*. The FAkLi showed significantly less efficacy than FAqLi ($p=0.0061$), particularly for *S. mutans*. For dosage levels, 250 μg mL^{-1} and 500 μg

mL^{-1} were significantly more effective than 62.5 μg mL^{-1} ($p<0.001$), and 500 μg mL^{-1} was more effective than 125 μg mL^{-1} ($p=0.000006$). *Escherichia coli* exhibited significantly less inhibition compared to *S. aureus* ($p<0.001$) and *S. mutans* ($p=0.0389$), while *E. faecalis* showed intermediate inhibition levels. Besides, FAkBe exhibited the lowest inhibition for *S. mutans*, while FAqLi was the most consistent across all bacteria, with the highest median inhibition values.

Polysaccharides are major structural components that may constitute up to 50% of the dry weight of fungal fruiting bodies (Arango and Nieto, 2013). In this study, *B. edulis* was composed of 16.04 g of polysaccharides per 100 g of dry biomass, including the aqueous and alkaline fraction, while *L. indigo* comprised 16.42 g of polysaccharides per 100 g of dry biomass, including both fractions. Rathore *et al.* (2017) reported a direct relationship between biomass production and polysaccharide concentration, suggesting that biomass accumulation plays a key role in polysaccharide yield, particularly under natural growth conditions where substrates may induce the synthesis of enzymes involved in metabolite production (Ooi and Liu, 2000), which makes wild mushrooms a potential source of metabolites (Arango and Nieto, 2013).

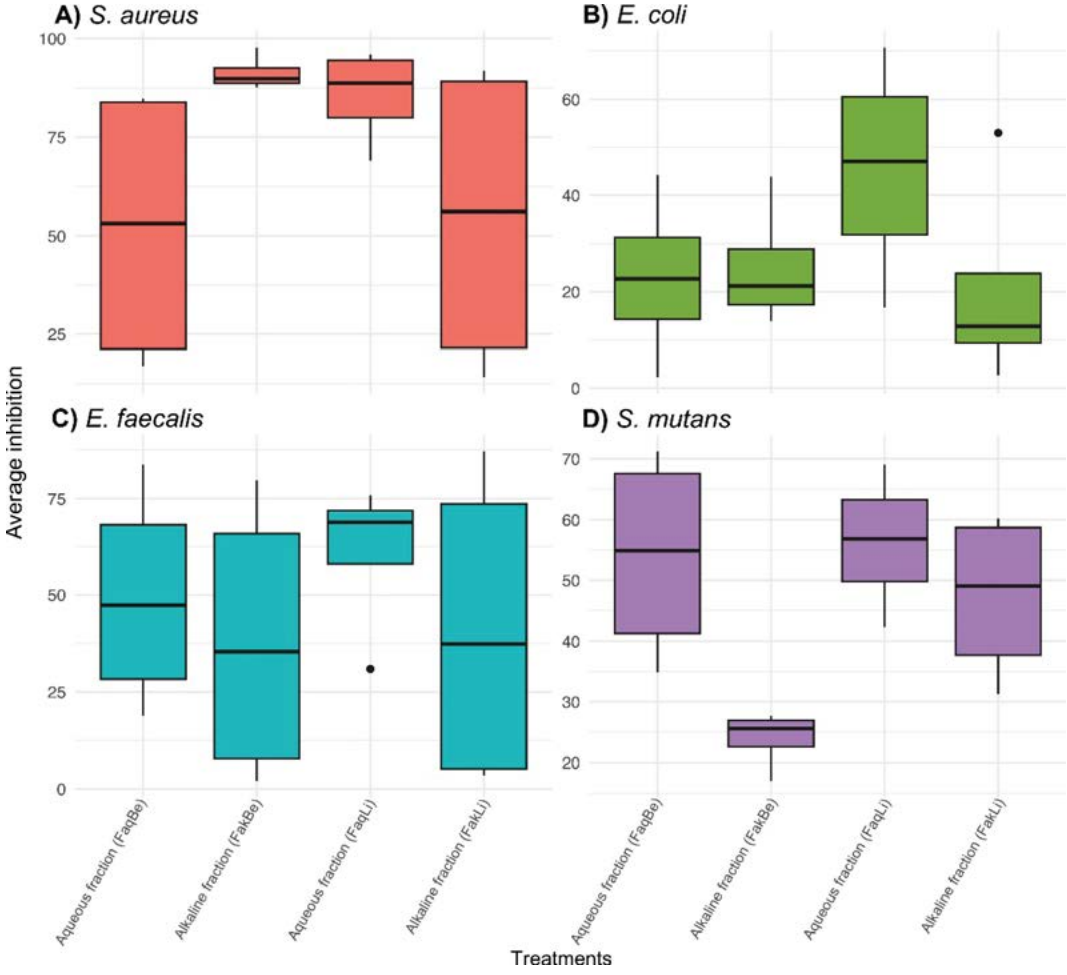

Figure 3. Tukey's post-hoc test of fractions from *Boletus edulis* and *Lactarius indigo*.

The concentration of polysaccharides can vary due to various factors such as substrate and extraction and purification methods. This was reported by Sari *et al.* (2017), who found that wild fruiting bodies of *B. edulis* contained 57.9 g of polysaccharides per 100 g of dry biomass in the pileus and 16.88 g per 100 g in the stipe. On the other hand, López-Vázquez *et al.* (2017) reported concentrations of polysaccharides present in fruiting bodies of *L. indigo* of 8.8 g of polysaccharides per 100 g of dry biomass. However, the presence of other compounds within the polysaccharide extracts cannot be ruled out, as the proposed method represents an efficient and low-cost alternative for extraction; nevertheless, it does not guarantee the complete removal of residual compounds during the extraction and purification processes.

Some *in vivo* studies have shown in which polysaccharides increase their resistance to bacteria by activating non-specific phagocytes of the immune system (Wang and Wang, 1997); however, the antibacterial activity of polysaccharides at the *in vitro* level remains to be described in detail. The bioactivity of polysaccharides could therefore be due to a direct effect on cells (Endo *et al.*, 2010). Several studies have demonstrated different mechanisms through which polysaccharides exert direct effects on bacteria, such as preventing bacterial adhesion, interfering with intracellular metabolic pathways, and altering or degrading plasma membranes and cell walls that are essential for bacterial growth. In addition, certain polysaccharides can inhibit bacterial enzymes and promote the production of antimicrobial compounds (Cheng *et al.*, 2024; Liang *et al.*, 2024).

Specific mechanisms have also been described for EPS and IPS extracts, which exhibit stronger antibacterial activity against Gram-positive bacteria (*e.g.*, *E. faecalis*), attributed to a greater affinity resulting from the absence of an outer membrane composed of lipopolysaccharides or a phospholipid layer, thereby facilitating polysaccharide penetration (Norhisham *et al.*, 2025). Therefore, the polysaccharides obtained from *B. edulis* and *L. indigo* may exert direct antibacterial effects on the evaluated strains. In this context, the antibacterial activity observed in this study may be associated with the physicochemical properties and structural characteristics of the extracted polysaccharides. According to Karácsonyi and Kuniak (1994), the bioactivity of the polysaccharides is related to the characteristics of the structure, its properties of solubility and the differences between molecular masses. It should be noted that polysaccharides can be coupled to a protein, so they have the ability to form supramolecular structures capable of increasing bioactivity through the formation of secondary structures (Chen and Seviour, 2007).

The concentration of polysaccharides presented in the fruiting bodies of both species was higher in the alkaline fraction. This may be attributed to the 2% NaOH extraction process, which disrupts the fungal cell wall and facilitates the release of alkali-soluble polysaccharides (Tseng *et al.*, 2008). This despite the fact that there are several studies that report the aqueous fraction to normally present higher bioactivity (Xiao *et al.*, 2004), probably due to the mechanisms mentioned above. Nevertheless, a concentration-dependent inhibitory effect was clearly observed for both aqueous and alkaline fractions.

CONCLUSIONS

The polysaccharides obtained from the wild fruiting bodies of *B. edulis* and *L. indigo* showed significant antibacterial activity against the evaluated bacterial strains; *S. mutans*, *S. aureus*, *E. coli* and *E. faecalis*. In general, higher dosage levels resulted in significantly greater inhibition across all treatments, with 500 μg mL^{-1} showing the strongest effect. Likewise, the findings obtained in this study suggest that FAqLi is the most promising treatment and that higher doses are generally more effective in inhibiting bacterial growth, whereas FAkBe exhibited the lowest inhibition, particularly against *S. mutans*. On the other hand, *E. coli* was the least responsive to treatment, while *S. aureus* and *S. mutans* showed the highest inhibition rates.

Finally, it is important to recognize that wild species such as *B. edulis* and *L. indigo* are of high nutritional value as well as presenting an alternative for obtaining metabolites of medicinal, nutraceutical and biotechnological importance.

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