



Polyphasic identification, total phenolic compounds and antioxidant activity of selected Agaricomycetes from Brazilian and Chilean environments

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Abstract

The study aimed to investigate the antioxidant potential and total phenolic content of Agaricomycetes species from Brazilian and Chilean environments using a polyphasic approach that combined morphological, molecular, and matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS) analyses. Fourteen fungal strains, including newly collected specimens and isolates from the URM culture collection, were examined, yielding 10 species across five genera. Biochemical assays revealed variability in phenolic compound production, with *Schizophyllum commune* (URM 8349), *Stereum hirsutum* (URM 8851), and *Trametes versicolor* (URM 8852) exhibiting the highest concentrations. Antioxidant activity was assessed using three methods (TEAC, DPPH, and CUPRAC), with *T. versicolor* (URM 8852) consistently showing the most effective antioxidant performance across all assays. The findings support the biotechnological potential of Agaricomycetes as promising natural sources of antioxidant compounds for applications in the food, pharmaceutical, and cosmetic industries.

Keywords – Basidiomycota – Biotechnology – MALDI-TOF MS – Phylogenetic

Introduction

Agaricomycetes is the largest class of Basidiomycota, to which belong the mushrooms, polypores, jelly and coral fungi, earth stars, bird's nest fungi, false truffles, boletes, among others (Watkinson et al. 2015, Hibbett et al. 2006). Species are mostly saprotrophs, but also ectomycorrhizal and parasitic (Sánchez-García et al. 2020, Sato 2024). Some species are edible, while others are toxic (Mleczek et al. 2021, Drewinski et al. 2024).

The identification of Agaricomycetes combines morphological and molecular methods, initially based on macro and microscopic characteristics and, in recent years, using DNA

sequences, such as ribosomal and protein-coding genes (Hibbett et al. 2014). Thus, an integrative approach combining different taxonomic methodologies is essential for robust and modern identification of this fungal group (Hibbett et al. 2014, Li et al. 2019, Song et al. 2021, Zhao & Xu 2023). Among the most reliable methods for rapid and straightforward identification, differentiation, and classification of microorganisms is the matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS), which has gained prominence in recent years (Chalupová et al. 2014, Santos et al. 2021, Calderaro & Chezzi 2024). Although studies are mostly focused on the identification of medical, sanitary supervision, and the agricultural industry species (Horisawa & Iwamoto 2022), the use of MALDI-TOF MS in environmental Agaricomycetes has also been increasingly reported (Vasina et al. 2013, Tomé et al. 2019, Piarroux et al. 2021, Horisawa & Iwamoto 2022).

Agaricomycetes are widely used in research for biotechnological applications, due to several properties, among them the antioxidant activity of phenolic compounds (Campi et al. 2021, Elhusseiny et al. 2021, Jacinto-Azevedo et al. 2021, Santos & Carvalho 2021, Karakas et al. 2023). An antioxidant is a stable molecule that donates an electron to a rampaging free radical, can significantly delay or completely prevent the oxidation of substrate molecules, even at low concentrations, being formed by a heterogeneous set of substances such as vitamins, minerals, natural pigments, and enzymes (Halliwell 1996, Gulcin et al. 2010, Prevedello & Comachio 2021, Gulcin & Alwasel 2023). The diet must provide the antioxidants as the body cannot produce them (Ramassamy 2006, Yadav et al. 2014, Prevedello & Comachio 2021). Protection against free radicals can be enhanced by taking sufficient amounts of exogenous antioxidants, so natural sources of antioxidants have been the target of research in recent years, and fungi have emerged as a supplementary alternative (Yadav et al. 2014, Prevedello & Comachio 2021, Rani et al. 2021, Cheng et al. 2024).

Despite a well-documented species richness of Agaricomycetes in South America (Ryvarden 2004, 2015, 2016, Maia et al. 2015, Furci 2018, Nouhra et al. 2019), studies evaluating their total phenolic content and antioxidant activity remain limited; however, preliminary investigations involving specimens from Brazil (Rosa et al. 2020, Chilanti et al. 2021, Santos & Carvalho 2021, Miranda et al. 2024) and Chile (Jacinto-Azevedo et al. 2021, Abdala-Díaz et al. 2024, Villalobos-Pezos et al. 2024) have created a basis for further, more detailed exploration of the antioxidant potential of species from these areas. Thus, the objective of this study is to evaluate the phenolic compound concentrations and antioxidant activity of fungi collected in Brazil and Chile using distinct methods, and to assess the use of MALDI-TOF against morphological and molecular analyses.

Material & Methods

Collection and isolation

Agaricomycetes specimens were collected in Brazil and Chile (Table 1). A fragment of basidiomata was immersed in 2,5% sodium hypochlorite 70%, alcohol and sterilized water for 1 min., at each stage, and transferred to Petri dishes with Potato Dextrose Agar (PDA). A piece of the mycelium was subsequently transferred to another dish to avoid contamination (Cavalcanti 1972, Stalpers 1978, Motato-Vásquez et al. 2018, Ferreira-Silva et al. 2022). After being isolated, the specimens were deposited in the Micoteca URM, Universidade Federal de Pernambuco (UFPE), and in the Universidad de La Frontera (UFRO). Additionally, some isolates previously deposited in the Micoteca URM were requested and included in the analysis.

Biomass production

Isolates were grown in Erlenmeyer flasks with 200 mL of Potato Dextrose (PD). The flasks were put in aerobic conditions on a rotary shaker at 300 rpm for an average of 10 days at a temperature of 25°C. The mycelium was filtered, freeze-dried, macerated, and stored until the analysis was carried out.

Morphological analysis

The basidiomata were morphologically analyzed according to the length, width, thickness, insertion in the substrate, consistency, color, and characteristics of the abhymenial and hymenial surfaces, the context, and the margin (Kornerup & Wanscher 1978, Fidalgo & Bononi 1989). The microscopic analyses were performed by preparing sections mounted in 3% KOH and stained with 1% phloxin to observe hyphae and spores. Melzer's reagent was used to observe amyloid or dextrinoid reactions (IKI+/IKI-). The presence or absence of cyanophilic reaction was observed in preparations with lactophenol cotton blue (CB+/CB-).

Molecular genetic analyses

For molecular identification, fragments from the basidiomata were removed and stored at -20°C or at room temperature until DNA extraction. The fragments were homogenized in 2 mL tubes with Cetyltrimethylammonium bromide (CTAB) and glass beads. DNA was extracted using a modified method described in Góes-Neto et al. (2005). Polymerase Chain Reaction (PCR) amplification of the ITS region was performed using the primer pairs ITS1 and ITS4 (White et al. 1990). The PCR products were purified using the enzyme NucleoSAP (CELLCO), following the manufacturer's recommendations. Samples were sequenced at the Plataforma Tecnológica de Genômica e Expressão Gênica do Centro de Biociências, in the UFPE, Brazil. Cycle sequencing was conducted using the same primers as the amplification reactions (Moncalvo et al. 2000). All newly generated sequences were deposited in GenBank (Table 1).

Phylogenetic analyses

The sequences obtained were compared with those deposited in GenBank using the BLASTn tool. They were then aligned and edited using the "Multiple Alignment using Fast Fourier Transform" (MAFFT) version 7 and Molecular Evolutionary Genetics Analysis (MEGA) version 7 software (Kumar et al. 2016). The best-fit evolutionary model was estimated for the combined dataset using standard model selection (Kalyaanamoorthy et al. 2017), implemented in IQ-TREE v. 1.6.12 for the maximum likelihood analyses (ML) and ModelTest on TOPALi 2.5 for the Bayesian inference (BI). Phylogenetic trees were developed using maximum likelihood (ML) and Bayesian inference (BI). For ML, W-IQ-TREE with 1000 bootstrap resampling was used (Trifinopoulos et al. 2016), and the construction of the BI analysis was performed using MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003) runs for 1×10^6 generations. Statistical support for branches was considered informative with Bayesian posterior probabilities (pp) ≥ 0.8 and bootstrap (bs) and values $\geq 50\%$. Sequences of specimens representing the type species of the specimens here analysed were selected. *Dacrymyces stillatus* Nees was chosen as an outgroup following Hibbett (2006).

Table 1 Data on taxa used in the phylogenetic analyses inferred from ITS sequences.

Species	Voucher	Country	ITS	Reference
<i>Dacrymyces stillatus</i> Nees	CBS:195.48	France	MH856306	Vu et al. (2019)
<i>Fomitiporia chilensis</i> Rajchenb. & Pildain	CIEFAPcc519	Chile	MK131089	Rajchenberg et al. (2019)
<i>Fomitiporia chilensis</i>	URM 8853	Chile	OR501543	This study
<i>Lentinus crinitus</i> (L.) Fr.	DSH92N43C	Costa Rica	KP283495	Seelan et al. (2015)
<i>Lentinus crinitus</i>	URM 8114	Brazil	PP873651	This study

Table 1 Continued

Species	Voucher	Country	ITS	Reference
<i>Lentinus tricholoma</i> (Mont.) Zmitr.	CuTENN9591 SBI 1	Puerto Rico	AF516555	Unpublished
<i>Lentinus tricholoma</i>	URM 8351	Brazil	MW578794	Unpublished
<i>Schizophyllum commune</i> Fr.	olrim832	Sweden	KY352530	Smith et al. (2017)
<i>Schizophyllum commune</i>	URM 8020	Brazil	PP873654	This study
<i>Schizophyllum commune</i>	URM 8112	Brazil	PP873653	This study
<i>Schizophyllum commune</i>	URM 8349	Brazil	PP892253	This study
<i>Schizophyllum commune</i>	URM 8772	Brazil	PP873655	This study
<i>Stereum hirsutum</i> (Willd.) Pers.	FLAS-F-61078	USA	MH211730	Ibrahim et al. (2020)
<i>Stereum hirsutum</i>	URM 8851	Chile	OR501544	This study
<i>Trametes flavida</i> (Lév.) Zmitr.	MP19	Philippines	OR099745	Unpublished
<i>Trametes flavida</i>	URM 8773	Brazil	PP873649	This study
<i>Trametes lactinea</i> (Berk.) Berk. & Cooke	9V7/2	Thailand	GQ982888	Pinruan et al. (2010)
<i>Trametes lactinea</i>	URM 8113	Brazil	PP873648	This study
<i>Trametes lactinea</i>	URM 8350	Brazil	PP873647	This study
<i>Trametes sanguinea</i> (L.) Lloyd	BRFM 1114	French Guiana	JX082366	Berrin et al. (2012)
<i>Trametes sanguinea</i>	URM 8774	Brazil	PP873650	This study
<i>Trametes versicolor</i> (L.) Lloyd	PRM 900594	Czech Republic	AY684179	Tomsovský et al. (2006)
<i>Trametes versicolor</i>	URM 8852	Chile	OR501545	This study
<i>Trametes villosa</i> (Sw.) Kreisel	strain 579	Colombia	OM400545	Sánchez- Quitian et al. (2022)
<i>Trametes villosa</i>	URM 8022	Brazil	PP873646	This study

MALDI-TOF MS analyses

MALDI-TOF MS was used for fungal species classification and characterization based on both ribosomal proteins and lipid profiles, following the extraction protocol by Barião et al. (2023) and Stübiger et al. (2016), respectively, with modifications. 1 µL of the supernatant was pipetted in

MALDI plate, and 1 μ L of saturated solution of α -cyano 4-hydroxycinnamic acid diluted in 50% acetonitrile with 2.5% trifluoroacetic acid (TFA) was added. Mass spectra were obtained using a MALDI-TOF MS Autoflex Speed (Bruker Daltonics, Bremen, Germany) equipped with a smart beam laser source (334 nm). The analyses were performed in linear mode with positive polarity, acceleration voltage of 20 kV, and extraction delay of 220 ns. Each spectrum was collected as an average of 1200 laser shots with sufficient energy to produce good non-saturating spectra in the m/z range of 2000 to 20000 and in the m/z range of 300 to 2000. Before the analyses, the equipment was externally calibrated with the peptide calibration standard using the FlexControl 1.4 software (Bruker Daltonics, Bremen, Germany).

Extraction of phenolic compounds and determination of antioxidant activity

The quantification of total phenolic compounds was carried out using the Folin-Ciocalteu method, while the determination of antioxidant activity was evaluated through the Trolox Equivalent Antioxidant Capacity (TEAC), Cupric ion Reducing Antioxidant Capacity (CUPRAC), and DPPH free-radical scavenging assay (DPPH). The analyses followed Nahuelcura et al. (2022), with modifications.

Statistical Analysis

The statistical analyses were generated in R version 4.5.1 and RStudio 2025.05.1+513. Data were Z-transformed when necessary. Nonetheless, the results are presented in their original numerical scale. One-way ANOVA was used to test for differences among samples and methods. For variables with significant differences, the means were compared using the Tukey HSD multiple range test ($p < 0.05$) with the packages “agricolae”, “ggplot2”, “dplyr”, and “multcompView”.

Results

In total, two specimens were collected and isolated in Brazil and three in Chile (Fig. 1). The basidiomata of the collected specimens were morphologically identified up to genus, and the species confirmed through molecular analyses. Additionally, nine strains were requested from the Micoteca URM (Fig. 2) and included in the phylogenetic analyses, resulting in the identification of 10 species belonging to five genera. The dataset of ITS rDNA regions included 25 sequences with 741 nucleotide sites, 14 of which were from eight genera generated in the present study. The best evolutionary model estimated for the alignment was TPM3+F+G4 for ML and SYM+G for BI. The ML and BI analyses produced similar topologies, and the BI tree was chosen to represent the phylogenetic placement of the specimens (Fig. 3).

The presence of phenolic compounds was not detected for some isolates of *S. commune* (URM 8020, URM 8772), *T. villosa* (URM 8022), and *T. lactinea* (URM 8113). Among the isolates with positive results, *S. hirsutum* (URM 8851) (1,92 mg/g), *T. versicolor* (URM 8852) (1,59 mg/g) and *S. commune* (URM 8349) (1,17 mg/g) showed the highest, while *T. lactinea* (URM 8350) and *T. flavida* (URM 8773) the lowest regarding total phenolic compounds production (Fig. 4–7).

The antioxidant activity showed positive results in the three methods evaluated and the isolates showed significant values for each method tested (Fig. 4–7). In the method TEAC, *T. versicolor* (URM 8852) (4,32 μ mol/g TE), *L. tricholoma* (8351) (3,27 μ mol/g TE) and *S. hirsutum* (URM 8851) (3,19 μ mol/g TE) had the best results, while *S. commune* (URM 8020) (1,12 μ mol/g TE) and *S. commune* (URM 8112) (1,29 μ mol/g TE) had the worst. For DPPH method, *T. versicolor* (URM 8852) (2,76 μ mol/g TE) and *S. commune* (URM 8772) (2,44 μ mol/g TE) presented the best results, while *L. crinitus* (URM 8114) (0,81 μ mol/g TE) and *L. tricholoma* (URM 8351) (0,90 μ mol/g TE) were the worst. For CUPRAC, *T. versicolor* (URM 8852) (16,73 μ mol/g TE) and *F. chilensis* (URM 8853) (9,91 μ mol/g TE) showed the best results, while *S. commune* (URM 8020) (1,32 μ mol/g TE) and *S. commune* (URM 8772) (3,10 μ mol/g TE) the worst.

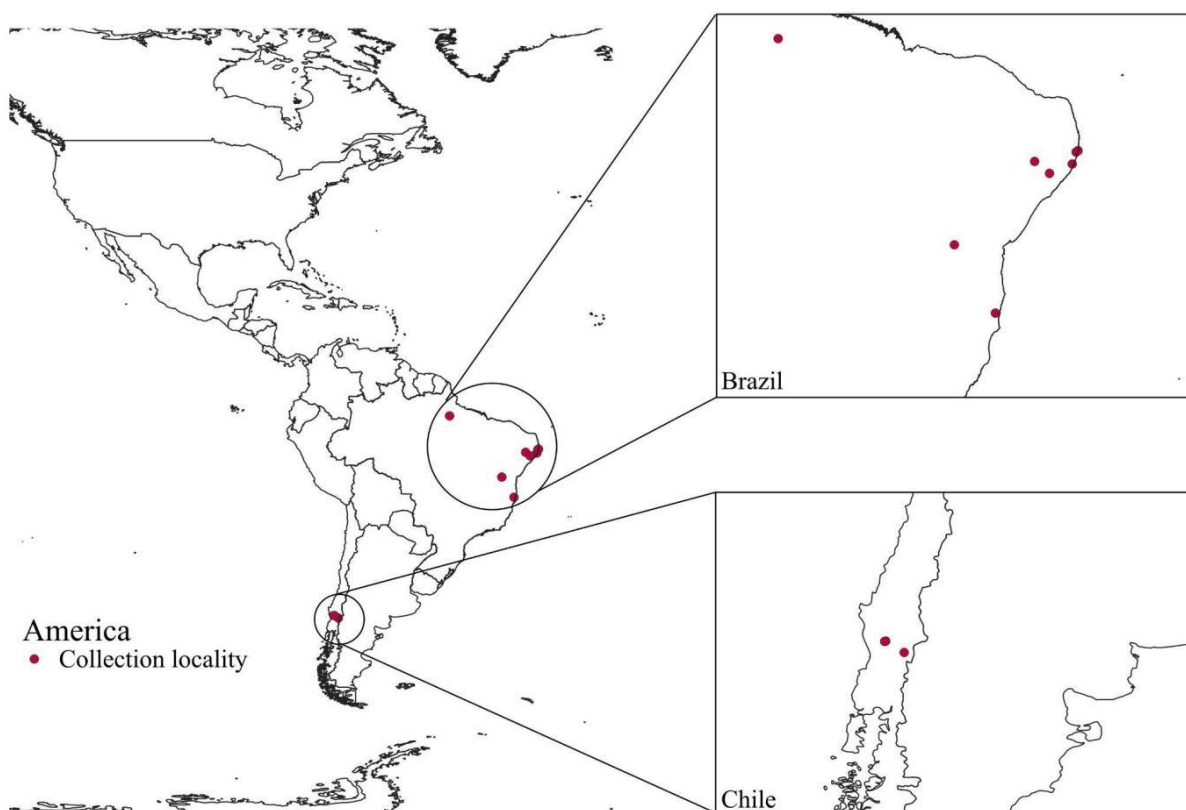


Fig. 1 – Collection locality of the specimens used in the study.

Discussion

The protein and lipid profiles of the isolates showed the presence of compounds in each specimen analyzed in MALDI-TOF MS. All species tested generated reproducible protein and lipid spectra (supplementary material) with a high number of intense signals. However, identification using this methodology was not useful, since the use of MALDI-TOF MS is more usual for identification of fungi of medical or agronomic interest (Oliveira et al. 2015, Santos et al. 2017, Robert et al. 2021, Alizadeh et al. 2021, Chen et al. 2021, Chun et al. 2022, Cruz et al. 2023) and studies using environmental specimens, mainly basidiomycetes, have not accumulated sufficient whole-genome data to allow selection of marker proteins or lipid peaks for characterizing fungal species in mass spectra using bioinformatics (Horisawa & Iwamoto 2022). Nonetheless, our results contribute to enriching information about the environmental specimens profile, using 14 strains of wood-inhabiting fungi.

Folin-Ciocalteu method is not specific for phenolic compounds and can also react with organic and inorganic substances (Rebelo et al. 2013, Chen et al. 2020), which is the reason why some isolates, with low concentration, values did not present favorable results. The Folin-Ciocalteu method can also detect tyrosine in proteins, and the basic mechanism is an oxidation/reduction reaction with the phenolic group being oxidized and the metal ion reduced (Agbor et al. 2014). Phenolic compounds were identified based on their spectroscopic characteristics.

The method TEAC is based on the scavenging of the relatively stable blue/green ABTS radical, converting it into a colorless product (Arts et al. 2003, Gómez-Maqueo et al. 2021). In the same way, DPPH is based on spectrophotometric measurements of the capacity of antioxidants to scavenge DPPH radicals (Gulcin & Alwasel 2023). Finally, the CUPRAC method is based on the absorbance measurement of Cu(I) neocuproine (Nc) chelate formed as a result of the redox reaction of chain breaking antioxidants with the CUPRAC reagent (Özyürek et al. 2011, Apak 2018).

All methods tested presented positive results, with DPPH being the method in which the isolates presented the most uniform values, with similar average, despite the highest values being detected using the CUPRAC method.

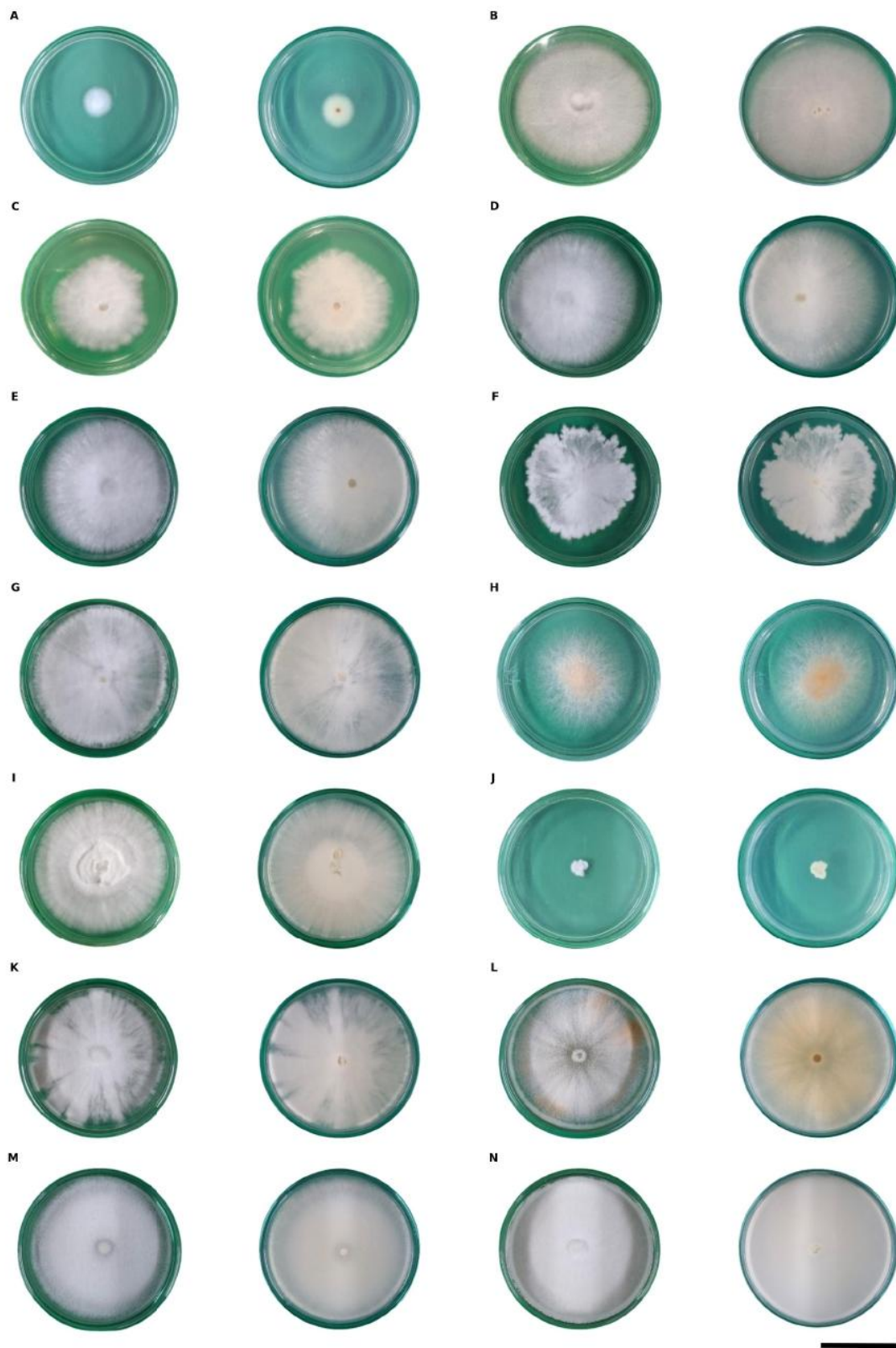


Fig. 2 – Culture characteristics of strains. Colonies grown for seven days in PDA (obverse and reverse). A *Fomitiporia chilensis* (URM 8853). B *Lentinus crinitus* (URM 8114). C *Lentinus tricholoma* (URM 8351). D *Schizophyllum commune* (URM 8020). E *Schizophyllum commune* (URM 8112). F *Schizophyllum commune* (URM 8349). G *Schizophyllum commune* (URM 8772). H *Stereum hirsutum* (URM 8851). I *Trametes flavida* (URM 8773). J *Trametes lactinea* (URM 8113). K *Trametes lactinea* (URM 8350). L *Trametes sanguinea* (URM 8774). M *Trametes versicolor* (URM 8852). N *Trametes villosa* (URM 8022). Scale bar: 5 cm.

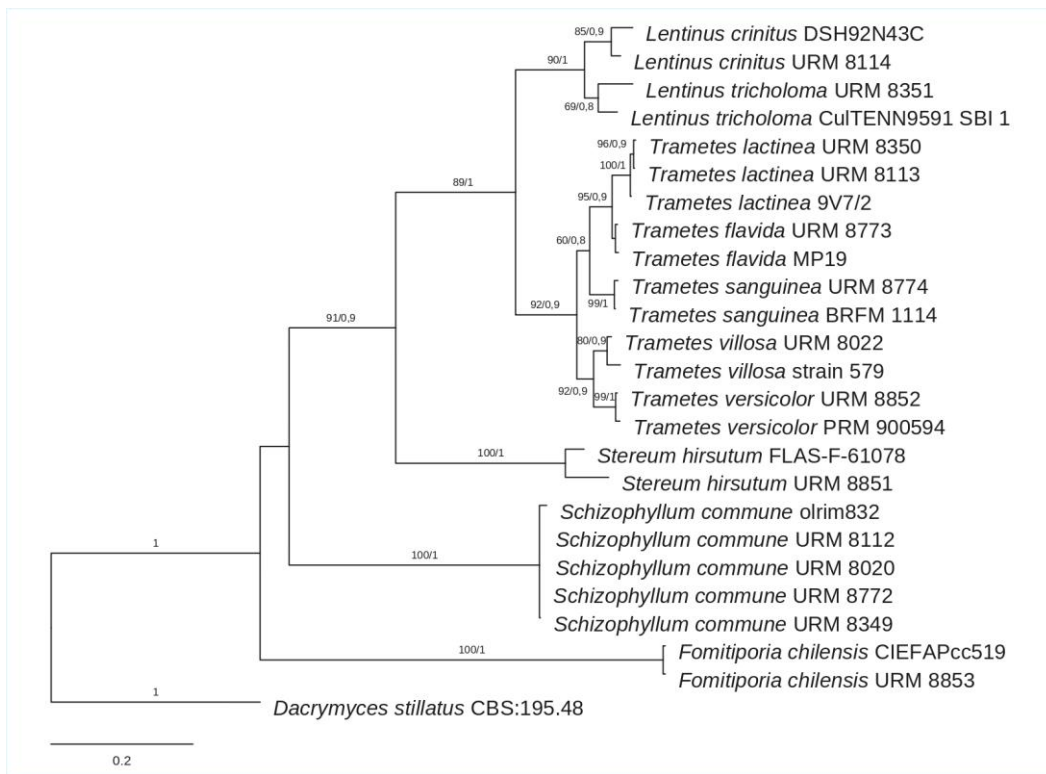


Fig. 3 – Bayesian inference (BI) tree from the ITS dataset of the specimens used in the study. Bootstrap values above 50 % and Bayesian posterior probability above 0.8 are shown.

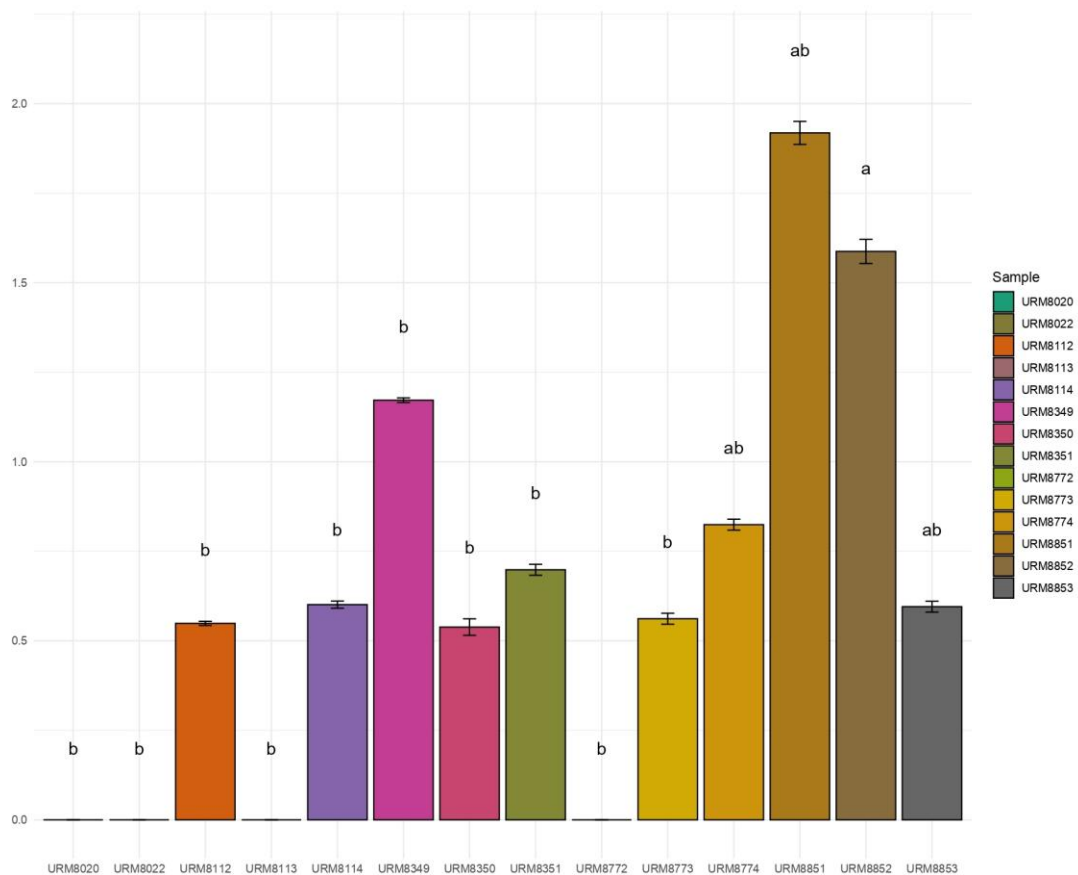


Fig. 4 – Total phenolic compound determined by the Folin-Ciocalteu method.

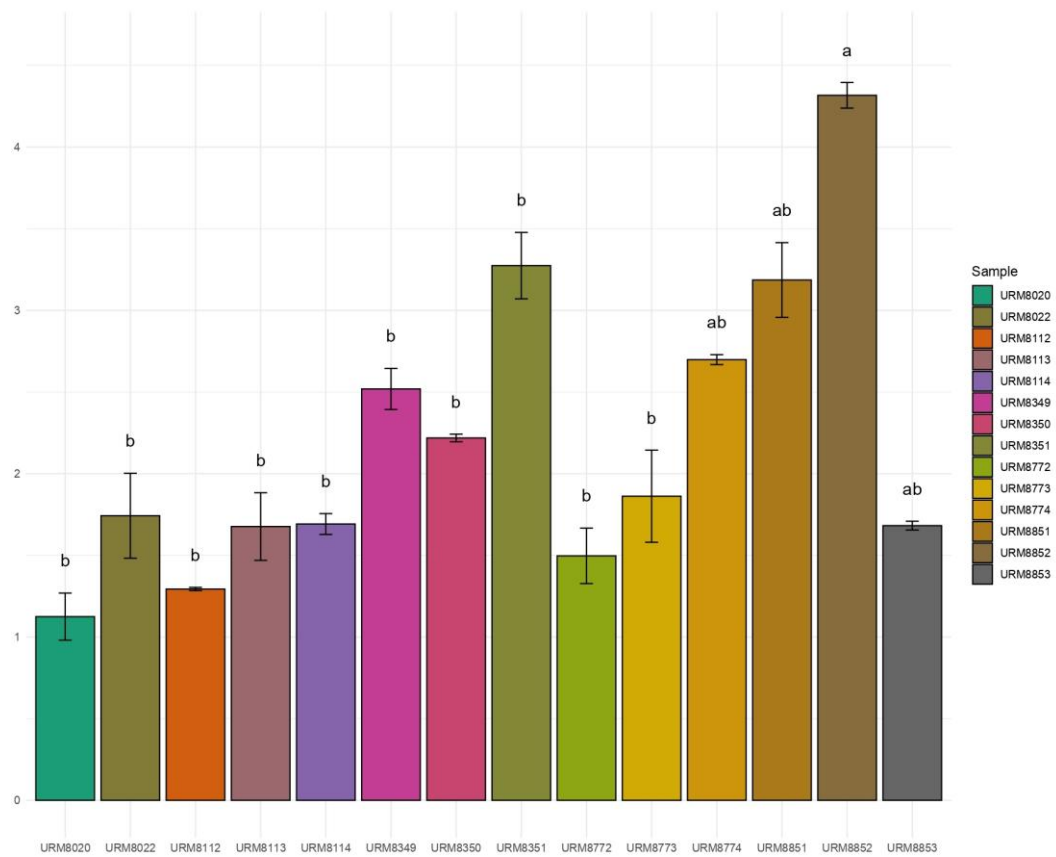


Fig. 5 – Antioxidant activity determined by the TEAC method.

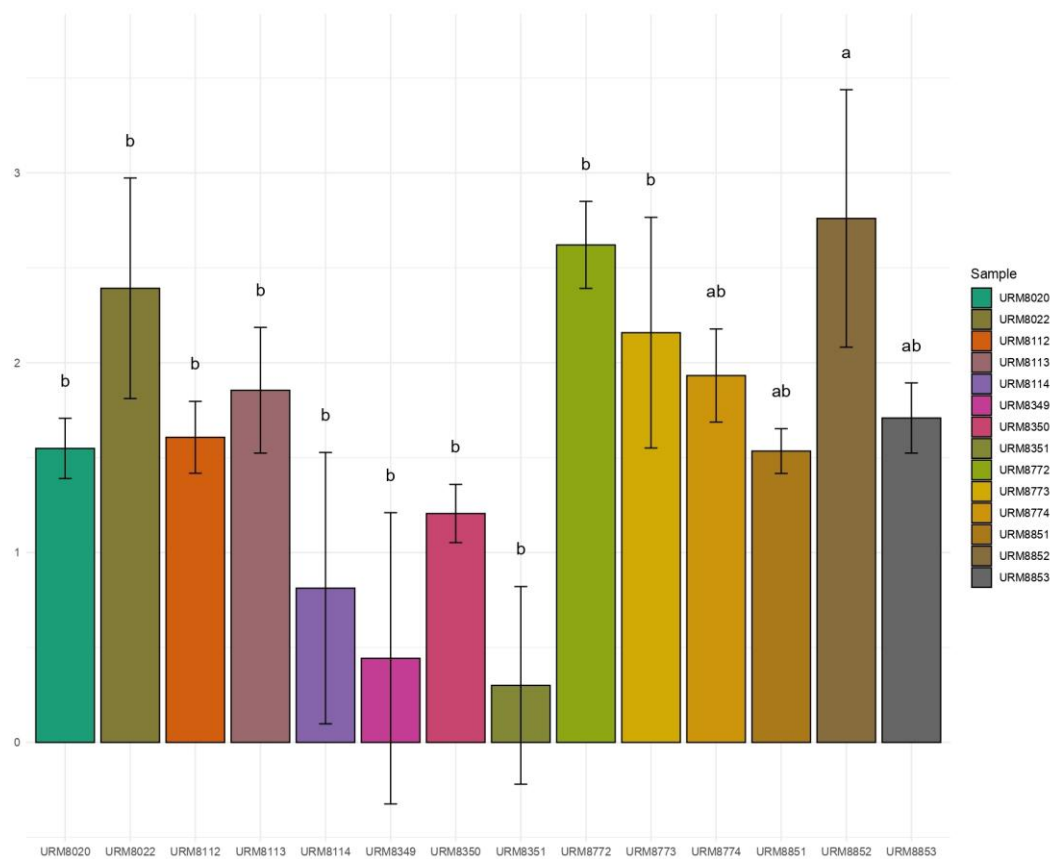


Fig. 6 – Antioxidant activity determined by the DPPH method.

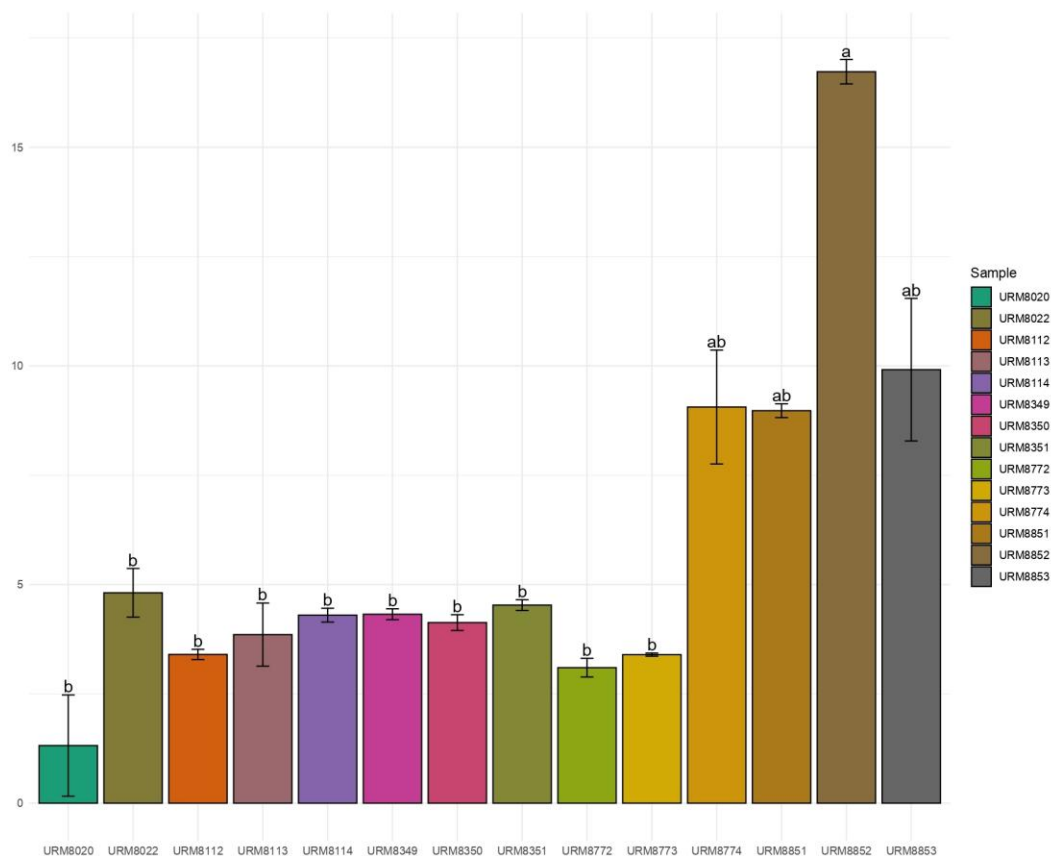


Fig. 7 – Antioxidant activity determined by the CUPRAC method.

Although not much explored in the environments of Brazil and Chile, other studies with species of the genera evaluated here corroborate our results. Among the species reported in the literature as edible, *Lentinus* and *Schizophyllum* are genera represented by species widely tested in biotechnological applications in relation to the evaluation of their antioxidant capacity, helping to understand the nutritional composition of these genera (Manjusha 2020, Bertéli et al. 2021, Ayimbila & Keawsompong 2021, Halabura et al. 2023, Naskar et al. 2023, Razak et al. 2024, Bing et al. 2024). In studies about *Lentinus* species, *L. fasciatus* Berk. showed $180.78 \pm 4.04 \mu\text{g/mL}$ of antioxidant activity by the DPPH method (Naskar et al. 2023), while *Lentinus arcularius* (Batsch) Zmitr. presented values of up to $72 \pm 0.02 \text{ mg/mL}$ in the mycelial extract (Yen et al. 2022). Similarly, *S. commune* is a cosmopolitan species, also known for its edibility and antioxidant capacity (Nuinamwong et al. 2024, Razak et al. 2024, Li et al. 2025). Among some tested samples, *S. commune* showed the strongest antioxidant activity against DPPH, with an IC_{50} of $49.34 \pm 0.65 \mu\text{g/mL}$ in ethanolic extract and $3.83 \pm 0.33 \text{ mg/mL}$ for DPPH and $2.38 \pm 0.45 \text{ mg/mL}$ for ABTS in water extract of mycelium (Razak et al. 2024).

Fomitiporia, *Stereum*, and *Trametes* are not commonly consumed as food (Drewinski et al. 2024), but several studies show their antioxidant activity (Smith et al. 2015, Zan et al 2015, Zengin et al. 2016, Liu et al. 2017, Çayan et al. 2019, Kim et al. 2021, Aranha et al. 2022, Mustafin et al. 2022). Despite little information available for the genus, *F. ellipsoidea* B.K. Cui & Y.C. Dai and *F. punctata* (P. Karst.) Murrill are species that present antioxidant compounds, which led them to be classified as natural sources of these compounds in China (Zan et al. 2015, Liu et al. 2017). *Fomitiporia chilensis* has already been shown to have antioxidant capacity in a previous study (Abdala-Díaz et al. 2024), with antioxidant activity evaluated at different polysaccharide concentrations present in the species. Likewise, species in *Stereum* had demonstrated good antioxidant activity by DPPH, ABTS, and CUPRAC methods (Çayan et al. 2019), with *S. hirsutum* having antioxidant capacity in both basidioma and mycelial extracts (Mišković et al. 2021, Yang et al. 2022, Goppa et al. 2023).

Among the genera discussed here, *Trametes* is the one that presents the most results among polypore fungi in relation to antioxidant capacity with different methodologies, making species of this genus promising options in the biotechnological process of obtaining these compounds (Smith et al. 2015, Zengin et al. 2016, Kim et al. 2021, Aranha et al. 2022, Mustafin et al. 2022). The results of our study link with some previous findings on filamentous fungi and their antioxidant activity, but, in macroscopic basidiomycetes, the analyses are mostly carried out by the basidioma and not by isolates (Smith et al. 2015, Sugiharto et al. 2016, Zengin et al. 2016, Knežević et al. 2018, Çayan et al. 2019, Rašeta et al. 2020, Kim et al. 2021, Tangjitjaroenkun & Tangchitharoenkhul 2020, Bertéli et al. 2021, Zakariya et al. 2022, Almustafa & Yehia 2023).

This study advances the knowledge about of neotropical wood-decaying fungi through the integration of morphological and ITS-based molecular data, while demonstrating their biotechnological potential as sources of phenolic compounds with significant antioxidant activity. Our results also support the effectiveness of the analytical methods used to evaluate total phenolic content and antioxidant activity in specimens collected across diverse environments in Brazil and Chile, highlighting their promising applications in industrial sectors, particularly as food and pharmaceutical additives, and reinforcing the relevance of these fungi for applied research and the sustainable exploitation of fungal diversity.

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