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Microarthropod Assemblages on Edible and Toxic Mushrooms in Northwestern Patagonia: Influence of Hymenophore Structure and Fungal Toxicity

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Abstract

We investigated microarthropod communities associated with 20 mushroom species in Northwestern Patagonia, including both edible and toxic fungi. Our study examined whether hymenophore structure (lamellar vs. tubular) and edibility or toxicity influence microarthropods abundance, richness, and diversity. Over 65,000 individuals were collected, representing 98 species. Collembola and Oribatida were identified to species level. Mushrooms with lamellar hymenophores supported higher total abundance and greater Diptera richness and diversity, while tubular fungi harbored significantly more Acari. Contrary to our initial expectation, the toxic species *Amanita muscaria*, exhibited high diversity. These findings highlight the role of mushrooms as ecological hubs for arthropod diversity, regardless of their edibility our results provide new insights into the role of fungal traits in structuring microarthropod assemblages and suggest avenues for further research on fungal–arthropod networks in temperate forests.

Keywords Agaricus | mushroom | Collembola | Oribatida | Microarthropod

1 Introduction

Edible mushrooms represent an important nutritional resource, particularly in forested regions, where frequent rainfall allows fungal growth. In cities located near natural rainforests, mushroom foragers often capitalize on this resource. This trend is especially prominent in the forested landscapes of Northwestern Patagonia in the Andes. Concerns arise when humans harvest mushroom sporocarps for consumption, particularly when they are eaten fresh or after being air-dried. These concerns stem not only from the inherent toxicity of some mushroom species but also from the potential for pathogen dispersal, facilitated by the infestation of certain arthropod groups.

As part of natural ecosystems, mushrooms provide both shelter and a vital food source for many microarthropods such as fly larvae, mites, and springtails. As evidenced by numerous studies, mushrooms constitute important feeding and oviposition resources for Diptera and a wide range of arthropods (O'Connell & Bolger 1997a, 1997b, Krivosheina 2008, Palacios-Vargas & Gómez-Anaya 1994). Fungal structures possess defensive traits that can influence colonization by microarthropods. For instance, Collembola grazing on spores and hyphae can stimulate defensive mechanisms, such as the protective

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function of cystidia (Nakamori & Suzuki 2007, Nakamori 2009). Some studies have also reported highly specific associations, where certain Collembola are restricted to the tubular hymenophores of Polyporales (Vázquez & Palacios-Vargas 1996). These interactions can shape both arthropod community structure and fungal reproductive success.

Previous research on interactions between edible mushrooms and animals in Northwestern Patagonia have mainly focused on mammals dispersing hypogeous fungi (Nouhra et al. 2005, Pérez Calvo et al. 1989, Núñez et al. 2013). Despite the presence of fossil evidence showing complex interactions among arthropods, fungi, and trees (García Massini et al. 2012, Greppi et al. 2021), as well as reports of entomopathogenic fungi in Patagonian provinces (Sosa Gómez et al. 2010), studies explicitly addressing arthropods inhabiting mushrooms in Patagonia remain scarce.

Given this background, we aimed to investigate the role of different mushroom species—particularly hymenophore structure (lamellar vs. tubular) and edibility— in shaping microarthropod communities in Northwestern Patagonia. The city of Bariloche and its surrounding environments offer favorable conditions for fungal development, including frequent precipitation, temperate forests, and pine plantations, providing an appropriate setting for a comparative study of microarthropod assemblages associated with mushrooms.

To address this primary question, we conducted a preliminary study examining the arthropod fauna associated with various identified edible mushrooms and one toxic species. We assessed the diversity, richness, and abundance of microarthropods by analyzing assemblages extracted from fungal sporophores collected in parks, squares, forests, and pine plantations within and around San Carlos de Bariloche city. Our objective was to identify the collected arthropods to the order or family level, with particular emphasis on achieving species-level identification for Collembola and Oribatida.

We assessed the ecological significance of microarthropod diversity associated with mushrooms, focusing on identifying which mushroom species support the greatest abundance and diversity. To achieve this, we examined two hypotheses to improve understanding of the relationships between microarthropods and both edible and poisonous mushrooms.

First, to assess the microarthropod communities associated with edible mushrooms, we quantified their abundance, richness, and diversity based on morphospecies, following the methodology of Derraik et al. (2010). Second, as in previous studies (Kun & Galende 2024), we focused on species-level identification specifically for typical soil and litter inhabitants—moss mites (Oribatida) and springtails (Collembola)—due to the near-complete taxonomic knowledge available for these groups (see Materials and Methods).

We carried out a correspondence analysis to search for associations between abundance data for identified microarthropods and mushrooms. After we compared 1) microarthropod communities found on lamellar hymenophores against those found on tubular hymenophores 2) microarthropod communities found edible against those found on poisonous mushroom *Amanita muscaria*.

Hypothesis 1: The shape and structure of mushroom hymenophores influence the attraction of microarthropods. We hypothesized that the species composition of microarthropods extracted would vary according to the hymenophore structure of each mushroom species. Specifically, we expected mushrooms with lamellar hymenophores to harbor more abundant and diverse microarthropod communities, due to their more open structure compared to species with tubular hymenophores.

Hypothesis 2: Edible mushrooms support more abundant and diverse microarthropod communities than toxic species. We hypothesized that toxic mushroom species would deter colonization through chemical defenses, resulting in lower abundance and diversity of associated microarthropod communities compared to edible species. Accordingly, we expected edible mushrooms to host more abundant and diverse microarthropod assemblages than Amanita muscaria, a toxic species.

2 Materials and methods

Study area and sampling

This study is based on extensive collections made by the authors, between 2023 and 2025. We collected 105 fungal sporocarps in and around San Carlos de Bariloche city. Sampling sites included urban gardens, parks, and surrounding forests such as Parque Municipal Llao Llao, Arroyo Casa de Piedra, Virgen de las Nieves, Lago Gutiérrez, Cerro Otto, Barrio Alto Jardín Botánico, Barrio La Cumbre, Dina Huapi, and the campus of the Universidad Nacional del Comahue. Duplicates of every fungal sample were deposited on BCRU herbarium.

Fungal examinations

Morphological and anatomical analyses were conducted using a dissecting and light microscope. Spores, basidia, cystidia and other structures characteristics were recorded. Chemical tests were applied when necessary.

Species identifications were confirmed against published keys and descriptions, and voucher material was curated at the herbarium.

2.1 Microarthropods studies

In the Zoology laboratory of the Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, microarthropods were extracted for identification. Fungal samples were placed in Tullgren funnels for 10 days at 20 °C, made with PET green bottles coated with black enamel, equipped with a 4 mm sieve. Each funnel was fitted with a 25-watt bulb and remained illuminated during the first three days. The arthropods were collected in 70% alcohol, counted and separated by main groups in different containers with Olympus CH5-260 and Zeiss BX40 microscopes. Representative specimens from each of the main groups mentioned earlier were mounted in Hoyer's medium. The remaining microarthropods are conserved in alcohol 70%.

Microarthropods, as defined in this study, are arthropods that typically pass through a 4 mm mesh size. Microarthropods were initially identified to the family level, and further Collembola and Oribatida were determined to the species level using identification keys and species descriptions. The bibliography used for identification included Krantz & Walter (2009) for families of mites, Bernava & Palacios-Vargas (2000), Heckman (2001), and Bellinger et al. (2024) for families of Collembola, and Amendt et al. (2010) for immature insects. Oribatid mites were identified to species level using keys and scientific descriptions from Hammer (1958, 1961, 1962a, 1962b), Balogh & Csiszár (1963), and Balogh & Balogh (1988, 1990). Since Hammer's and Balogh's investigations, scientific names for Oribatida have undergone changes, taxonomic names based on current sources we verified, as outlined by Subías et al. (2012). Collembola were identified at the species level by using available keys and descriptions (Bellinger et al. 2024, Heckman 2001). When detailed taxonomic information was limited, morphospecies as a subrogate of species following Derraik et al. (2010) were applied. We quantified the number of microarthropod specimens in each extraction discriminating by greater groups, we chose Collembola, Hexapoda orders and Mite orders, Myriapoda and Crustacea.

2.2 Statistical methods

All individuals were counted, and the different variables were calculated per fungal sample. To reduce potential bias from unequal sample sizes among fungal species, we calculated species-level means and used these averages in statistical analyses.

Multivariate exploratory analysis using Principal Component Analysis (PCA) was performed with STATISTICA software (version 7.0; StatSoft, Inc., www.statsoft.com). Abundance data were $\log_{10}$-transformed prior to the PCA.

2.3 Testing Hypothesis 1:

We compared the abundance, species richness, and diversity of microarthropods associated with fungi bearing lamellar hymenophores versus those with tubular hymenophores. For each group, we calculated the average values of community parameters—abundance, richness, and diversity—by pooling data from all species with the same hymenophore type. For multiple comparisons, we conducted Kruskal Wallis test with Post-Hoc Dunn's test using a Bonferroni correction.

2.4 Testing Hypothesis 2:

We compared the abundance, species richness, and diversity of microarthropods associated with *Amanita muscaria* versus edible mushrooms. For each group, we calculated the average values of community parameters—abundance, richness, and diversity—by pooling data from all species within each hymenophore type.

To assess differences in microarthropod communities, we used ANOVA. When assumptions of normality or homoscedasticity were not met, we applied the Kruskal-Wallis test. For multiple comparisons, we conducted Kruskal-Wallis test with Post-Hoc Dunn's test using a Bonferroni correction.

3 Results

20 species of mushroom were collected, belonging to *Agaricus arvensis, Agaricus augustus*, *Amanita muscaria*, *Boletus putidus*, *Coprinopsis atramentaria, Coprinus comatus, Cortinarius magellanicus, Cortinarius xiphidipus, Cyttaria darwinii, Fistulina antarctica, Ganoderma australis, Gymnopilus junonius, Hydropus dusenii, Lactarius deliciosus, Pleurotus ostreatus*, *Rhizopogon roseolus, Suillus caerulescens, Suillus lakei, Suillus luteus* y *Tricholoma* sp.

A total of 65,302 microarthropods were collected from 105 fungal sporocarps, representing 98 taxa. Of these microarthropod taxa, 47 were identified to species level

(including 13 Collembola and 6 Oribatida), while the remaining were classified as morphospecies. Although a high number of microarthropods was collected, it is expected that even greater numbers could be obtained by omitting the use of the bulb light during the first three days of extraction. This approach aligns with common practice, which aims to establish a humidity gradient that helps preserve microarthropod viability long enough for them to reach the collecting jars.

The remaining 51 of microarthropod groups were identified to different levels as orders, families or genera and considered morphospecies in this study. The major groups included Collembola, Acari (Trombidiformes, Mesostigmata, Astigmatina, Oribatida) and Diptera with lower representation of Araneae, Coleoptera, Homoptera, Hemiptera, Lepidoptera, Protura, Thysanoptera, Psocoptera, and Neuroptera. Crustaceans such as *Porcellio* sp. and various myriapods were also present (Tab. 1). Nematodes and Annelids were also present but excluded from this study as these are not arthropods. Collembola and Oribatida were identified to species level. Among mites (Oribatida including Astigmatina) were identified *Anderemaeus magellanis, Brachioppiella pepitensis, Cuspidozetes armatus, Lanceoppia kovacsi, Loftacarus longicaudatus, Maculobates longiporosus, Membranoppia breviclava, Multioppia australis, Oppiella nova, Paraphauloppia altimontanoides, Physobates spinipes, Setoppia angustopili, Tectocepheus velatus, Tyrophagus putrescentiae, Zetomimus polpaicoensis* and *Zygoribatula excavata.* Among Trombidiformes mites were found families Eupodidae, Microtrombidiidae, Pygmephoridae, Rhagidiidae, Tarsonemidae, Tetranychidae, Tydeidae and for Mesostigmata, Macrochelidae, Parasitidae, Phytoseidae and Uropodidae. Among springtails (Collembola) were identified *Brachystomella parvula, Brachystomellides neuquensis, Ceratophysella armata, Ceratophysella denticulata, Hemisotoma termophila, Entomobrya lanuginosa, Entomobrya pseudodecora, Entomobrya* sp.*, Hypogastrura manubrialis, Isotoma subantarctica, Lepidocyrtus gisini, Ptenothrix* sp., and *Tullbergia meridionalis.*

Table 1. Community parameters of microarthropods in different mushroom species. ns: number of samples, n: abundance, S: richness; H': Shannon index.

		n		S		H`			
Mushroom species	**ns**	**Total**	**Average**	**Total**	**Average**	**Total**	**Average**	**Hymenophore**	**Edibility**
Agaricus arvensis	51	63,156	1,238.35	62	1.22	1.00	0.39	lamellar	edible
Agaricus augustus	1	161	161.00	7	7.00	0.57	0.57	lamellar	edible
Amanita muscaria	13	302	23.23	31	2.38	2.33	0.60	lamellar	inedible, toxic
Boletus putidus	2	8	4.00	2	1.00	0.38	0.00	tubular	edible
Coprinopsis atramentaria	1	106	106.00	5	5.00	0.72	0.72	lamellar	inedible
Coprinus comatus	1	32	32.00	6	6.00	1.62	1.62	lamellar	edible
Cortinarius magellanicus	1	44	44.00	9	9.00	1.39	1.42	lamellar	edible
Cortinarius xiphidipus	1	1	1.00	1	1.00	0.00	0.00	lamellar	edible
Cyttaria darwinii	1	36	36.00	3	3.00	0.81	0.81	fleshy stroma	edible
Fistulina antarctica	1	21	21.00	2	2.00	0.41	0.41	tubular	edible
Ganoderma australis	1	84	84.00	10	10.00	1.20	1.20	tubular	inedible
Gymnopilus junonius	2	11	5.50	2	1.00	0.66	0.64	lamellar	inedible
Hydropus dusenii	1	744	744.00	2	2.00	0.01	0.01	lamellar	edible
Lactarius deliciosus	2	35	17.50	6	3.00	1.48	1.27	lamellar	edible
Pleurotus ostreatus	1	15	15.00	1	1.00	0.00	1.00	lamellar	edible
Rhizopogon roseolus	3	141	47.00	3	1.00	0.94	0.12	glebal	edible
Suillus caerulescens	1	2	2.00	1	1.00	0.00	0.00	tubular	edible
Suillus lakei	4	62	15.50	11	2,75	1.37	0.69	tubular	edible
Suillus luteus	7	223	31.86	15	2.14	1.00	1.14	tubular	edible
Tricholoma sp.	2	118	59.00	10	5.00	1.57	1.39	lamellar	inedible
Total	97	63,302							

We used the ecomorphological index EMI categories (Parisi et al. 2005) to further classify Collembola. Although recorded in low numbers, the soil indicator species *L. gisini* and *Ptenothrix* sp. can be classified within EMI category 1 (Parisi et al. 2005), corresponding to "epigeic forms, middle to large size, complex pigmentation present, long, well-developed appendages, well developed visual apparatus (eye spot and eyes)". In contrast, the more abundant species *C. armata*, *C. denticulata*, *B. neuquenensis*, *B. parvula*, and *H. manubrialis* fall under EMI category 3 (Parisi et al. 2005) which includes "small-sized taxa not strictly associated with leaf litter, exhibiting moderate pigmentation and a well-developed visual apparatus". *Hemisotoma termophila* is assigned to EMI category 4 (Parisi et al. 2005), representing "hemi-edaphic forms characterized by non-elongated appendages and a lightly pigmented cuticle". The rarely mushroom-associated species *T. meridionalis* corresponds to EMI category 7 (Parisi et al. 2005), indicative of "eu-edaphic forms lacking pigmentation and a furcula, possessing short appendages, pseudo-ocelli, and well-developed postantennal organs".

A total of 578 larvae belonging to the family Platypezidae (Diptera) were recovered exclusively from 15 fruiting bodies of *Agaricus arvensis*, suggesting a high degree of host specificity. Selected larvae were successfully reared to imagines and taxonomically identified as members of the genus *Lindneromya*.

Abundance, species richness, and Shannon diversity are summarized in Tab. 1. The highest total abundance was observed for *Agaricus arvensis* (63156 individuals), which also exhibited the greatest overall species richness (62 species). The highest Shannon diversity index was recorded for *Amanita muscaria* (2.33). In terms of sample averages, *A. arvensis* showed the highest mean abundance (1127.79), *Gymnopilus junonius* had the highest mean species richness (10), and *Coprinus comatus* demonstrated the highest average Shannon diversity (1.62).

The most abundant groups were Collembola, Acari (including Mesostigmata, Oribatida, and

Table 2. Abundance of microarthropods by higher-level taxa found in mushrooms.

	Mesostigmata	Oribatida	Trombidiformes	Collembola	Protura	Dermaptera	Diptera	Coleoptera	Homoptera	Hemiptera	Hymenoptera	Lepidoptera	Psocoptera	Thysanoptera	Crustacea	Myriapoda
A.arvensis	37	160	77	60913	0	3	1931	17	0	2	5	0	5	2	0	4
A.augustus	2	1	0	145	0	0	13	0	0	0	0	0	0	0	0	0
A.muscaria	1	59	46	174	0	0	14	2	1	0	0	1	0	4	0	0
B.putidus	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0
C.atramentaria	1	0	1	104	0	0	0	0	0	0	0	0	0	0	0	0
C.comatus	2	10	0	0	0	0	18	2	0	0	0	0	0	0	0	0
C.magellanicus	2	5	2	32	3	0	0	0	0	0	0	0	0	0	0	0
C.xiphidipus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
C.darwinii	0	0	0	0	0	0	23	13	0	0	0	0	0	0	0	0
F.antarctica	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0
G.australis	12	59	3	0	0	0	0	1	0	0	0	0	0	0	5	4
G.junonius	4	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H.dusenii	0	1	0	743	0	0	0	0	0	0	0	0	0	0	0	0
L.deliciosus	0	10	3	18	0	0	4	0	0	0	0	0	0	0	0	0
P.ostreatus	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0
R.roseolus	8	23	0	32	0	0	77	1	0	0	0	0	0	0	0	0
S.coerulescens	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
S.lakei	0	2	4	52	0	0	2	2	0	0	0	0	0	0	0	0
S.luteus	2	186	9	19	0	0	2	2	0	0	0	0	0	3	0	0
***Tricholoma* sp.**	2	38	0	76	0	0	0	2	0	0	0	0	0	0	0	0
Total	73	561	145	62339	3	3	2100	42	1	2	5	1	5	9	5	8

Trombidiformes), and Diptera. Collembola was by far the most dominant group, with total counts exceeding the combined abundance of all other taxa by more than 100-fold. Collembola was mainly found on *Agaricus arvensis* (Tab. 2).

3.1 Principal component analysis

We focused on the abundance of four taxonomic groups: Collembola, Astigmatina, Oribatida, and Diptera. We applied a log(x + 1) transformation to the abundance data to improve visualization in the PCA. Two principal components explained more than 81 % of the total inertia. The first axis accounted for 58.40 % of the variance, while the second axis explained 23.63 % (Fig. 1). The ordination revealed three distinct clusters: the first comprised mushrooms related to Oribatida (*A. muscaria*, *L.deliciosus*, *S. luteus* and *Tricholoma* sp.), in the second group Collembola and Diptera clustered near *A. arvensis*, *A. augustus and R. roseolus,* a third group, consisting of the remaining mushroom species, was clearly distinct from both the first and second clusters and showed no close association with any of the major groups of microarthropods examined (Fig. 1).

In table 3 we show the comparison between lamellar and tubular hymenophore structure and between edible and inedible mushrooms for abundance, richness and Shannon´s diversity.

Fleshy stroma and glebal fungi were excluded from comparative analyses due to low sample sizes. Six comparisons gave significant differences. 1) Microarthropod and 2) Collembola abundances were nearly 100 times greater in lamellar hymenophores, supporting the first hypothesis. 3) Acari abundance was nearly four times greater on mushrooms with tubular hymenophores, contradicting the first hypothesis. 4) Diptera richness was four times higher on lamellar hymenophores and 5) Diptera diversity was ten times greater on lamellar hymenophores, supporting the first hypothesis. 6) Acari specific diversity

Table 3. Comparison of community parameters of microarthropods grouped by hymenophore structure and edibility. ns: number of samples, n: abundance, S: richness; H': Shannon index, SE: standard error, KW H: Kruskal-Wallis H statistic, df: degrees of freedom. Significant differences are shaded.

		n			S			H'		
	ns	Total	Average	SE	Total	Average	SE	Total	Average	SE
Microarthropods										
lamellar	79	64725	819,3		313	3,96	2,41	51,84	0,66	0,54
tubular	17	400	23,53		48	3,43	2,38	9,53	0,68	0,46
Comparison		**KW H= 3.869, df = 1, p = 0.049**			KW H= 0.699 df = 1, p = 0.403			KW H= 0.112 df = 1, p = 0.738		
Collembola										
lamellar	79	64734	787,51	2796,28	90	1,14	0,89	15,9	0,20	0,22
tubular	17	392	6,71	9,08	11	0,79	0,80	2,21	0,16	0,17
Comparison		**KW H=4.075, df = 1, p = 0.044**			KW H = 1.782, df = 1, p = 0.182			KW H = 0.618 df = 1 p = 0.432		
Acari										
lamellar	79	471	5,96	9,17	120	1,52	1,51	20,06	0,25	0,32
tubular	17	277	**19,79**	40,74	25	1,79	1,76	5,04	0,36	0,32
Comparison		**Anova F(1, 91) = 7.352, p = 0.008**			KW H = 0.282, df = 1, p = 0.595			KW H = 0.242 df = 1 p = 0.153		
Diptera										
lamellar		1996	25,27	59,09	67	**0,85**	1,01	10,95	**0,14**	0,20
tubular		4	0,29	0,73	3	0,21	0,58	0,5	0,04	0,09
Comparison		Anova F(1, 91) = 2.48, p = 0.119			**Anova F(1, 91) = 5.14, p = 0.026**			**KW H = 5.033 df = 1 p = 0.025**		
Microarthropods										
edible	79	64681	829,24	2840,13	292	3,74	2,35	49,08	0,63	0,53
inedible	21	621	32,68	34,99	81	4,26	2,45	2,77	0,15	0,21
Comparison		Anova F(1, 95) = 1.483 p = 0.226			KW H = 0.786, df = 1, p =0.375			KW H= 1.785 df = 1, p = 0182		
Collembola										
edible	79	61985	794,68	2813,72	81	1,04	0,84	19,11	0,25	0,33
inedible	21	354	18,63	30,58	21	1,11	1,05	1,65	0,09	0,22
Comparison		Anova F(1, 95) = 1.434 p = 0.234			KW H =2.383x10-5, df = 1, p = 0.996			KW H= 0.421, df = 1, p = 0.517		
Acari										
edible	79	546	7	17,37	110	1,41	1,43	19,11	0,25	0,33
inedible	21	233	12,26	19,65	41	2,16	1,86	7,6	**0,4**	0,31
Comparison		KW H= 2.748, df = 1, p = 0.097			KW H= 2.732, df = 1, p = 0.098			**KW H= 5.016, df = 1, p = 0.025**		
Diptera										
edible	79	2086	26,74	59,58	63	0,81	1,01	10,17	0,13	0,2
inedible	21	14	0,74	1,48	9	0,47	0,77	1,59	0,08	0,13
Comparison		Anova F(1,95) = 3.591, p = 0.061			KW H= 1.689, df = 1, p = 0.194			KW H = 0.607, df = 1, p = 0.436		

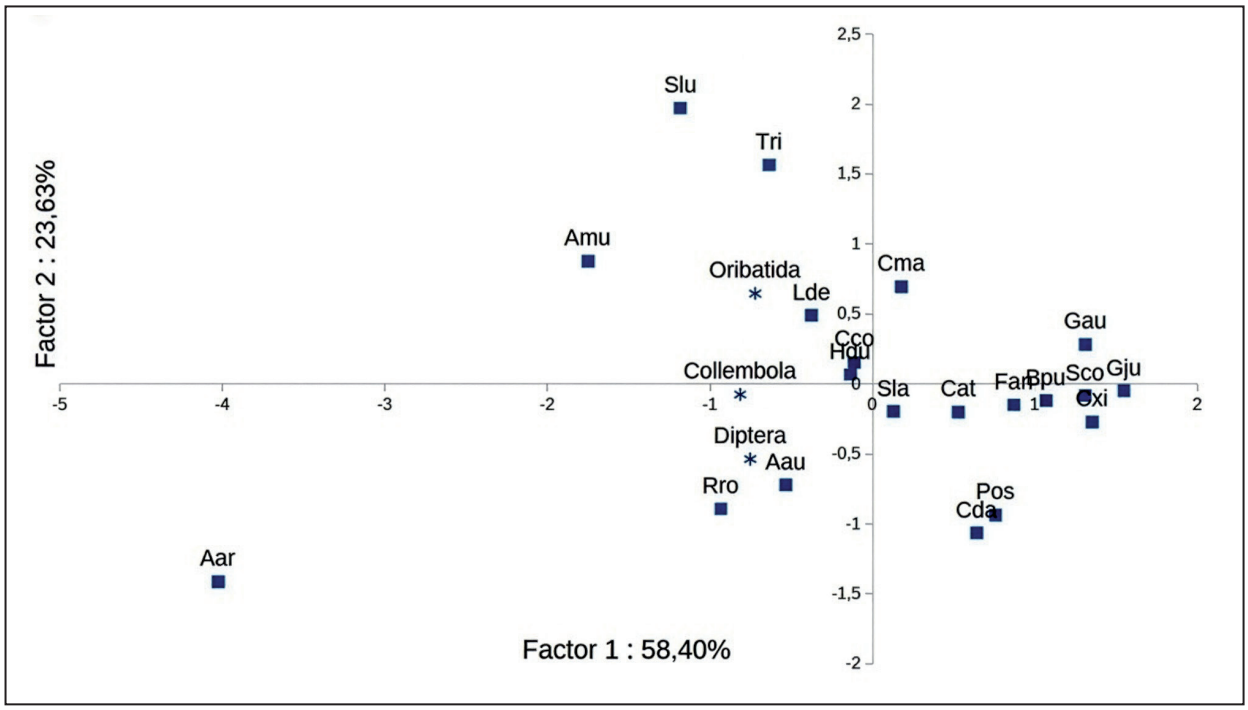

Figure 1. Principal Component Analysis (PCA) of the relationship between mushrooms and the abundance of dominant microarthropod groups. Abundance data were log(x + 1)–transformed prior to analysis to improve visualization. Aar: A. arvensis, Aau: A. augustus, Amu: A. muscaria, Bpu: B. putidus, Cat: C. atramentaria, Cco: C. comatus, Cma: C. magellanicus, Cxi: C. xiphidipus, Cda: C. darwinii, Fan: F. antarctica, Gau: G. australis, Gju: G. junonius, Hdu: H. dusenii, Lde: L. deliciosus, Pos: P.ostreatus, Rro: R. roseolus, Sco: S. caerulescens, Sla: S. lakei, Slu: S. luteus, Tri: Tricholoma sp. Raw abundance data were log10 transformed before the analysis.

was greater on inedible mushrooms, contradicting the second hypothesis (Tab. 3).

In figures 2 and 3 we plotted the abundance, the richness and the diversity of major microarthropods groups (Collembola, Acari and Diptera) comparing hymenophore structure type and edibility of mushrooms. See the annexed file for detailed comparisons.

A clear difference appears regarding Diptera abundance, richness and diversity were lower in tubular mushrooms, supporting the first hypothesis (Fig 2). Collembola shows higher numbers in edible mushrooms than Diptera in edible and indelible mushrooms (Fig. 3). Acari show higher richness and diversity than Collembola and Diptera in inedible mushrooms, contradicting the second hypothesis (Fig. 3).

Kruskal–Wallis multiple comparisons of abundance indicated a statistically significant difference ($H = 8.94$, $P = 0.030$). This pattern was primarily driven by Collembola, which were significantly more abundant in lamellar hymenophores compared to tubular ones. In contrast, Oribatida did not show significant differences in abundance with respect to hymenophore type or relative to Collembola abundance in tubular hymenophores (Fig. 4).

Given that the observed differences in Acari abundance contradicted our initial hypothesis—except in the cases of Collembola and Diptera—we considered that body size might influence access to tubular hymenophores. To test this, we measured the maximum body length (n = 3) of the six most abundant Oribatida (Acari) and the six most abundant Collembola. The comparison showed that Oribatida found in mushrooms were generally smaller than Collembola, suggesting that their reduced body size may facilitate access to the pores of tubular mushrooms. This observation was supported by statistical analysis (Anova: $F(1, 10) = 36.60$, $p = 0.00012$; Tab. 4, Fig. 5).

4 Discussion

Our study demonstrates that both hymenophore structure and fungal edibility influence the assemblages of microarthropods inhabiting mushrooms in Northwestern Patagonia. Although Collembola dominated some samples, abundance and diversity patterns varied consistently across fungal traits. *Agaricus arvensis* primarily attracted Diptera and Collembola, while Oribatida occurred only sparsely in a few mushrooms.

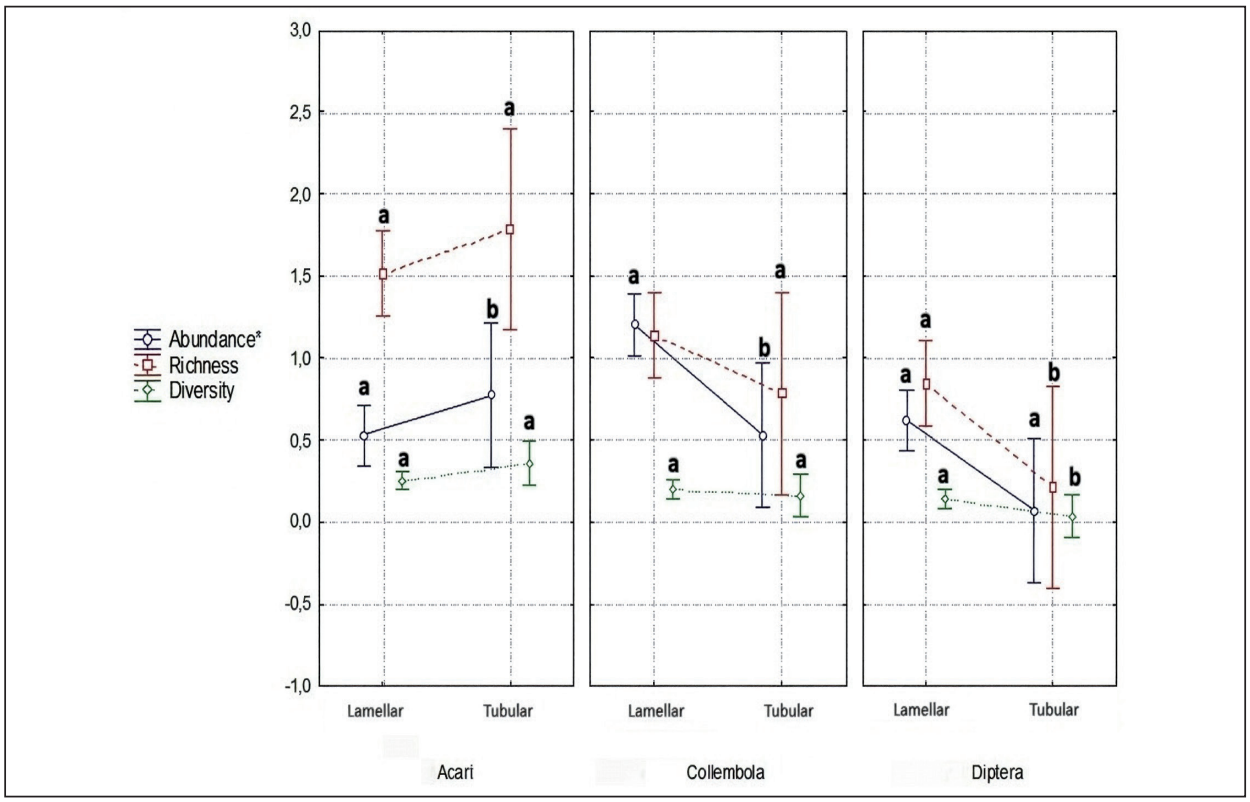

Figure 2. Abundance, Richness and Diversity of major groups according to mushroom hymenophore type, lam: lamellar type, tub: tubular type. Abundance data are log 10 transformed, different letters indicate significant differences between hymenophore type. Points represent mean values. Vertical bars denote 95 % confidence intervals.

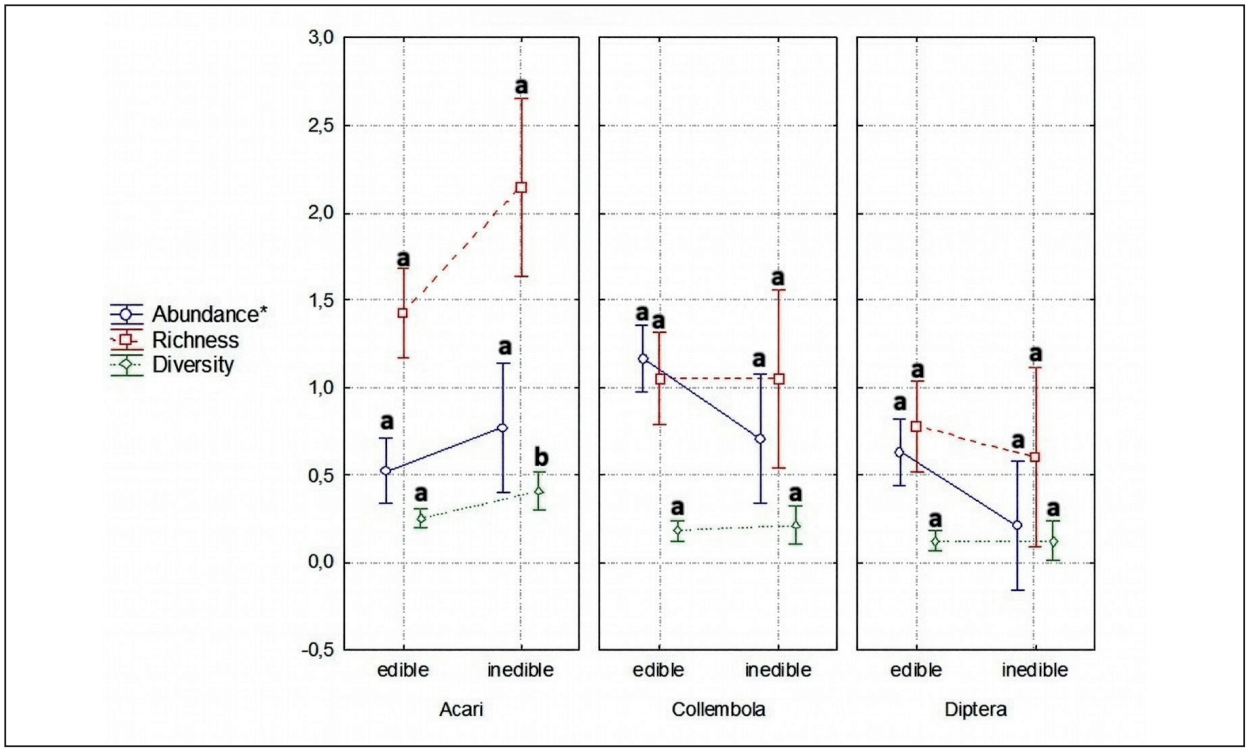

Figure 3. Abundance, Richness and Diversity of major groups according to mushroom edibility, abundance data are log 10 transformed, different letters indicate significant differences between edibility. Points represent mean values. Vertical bars denote 95% confidence intervals.

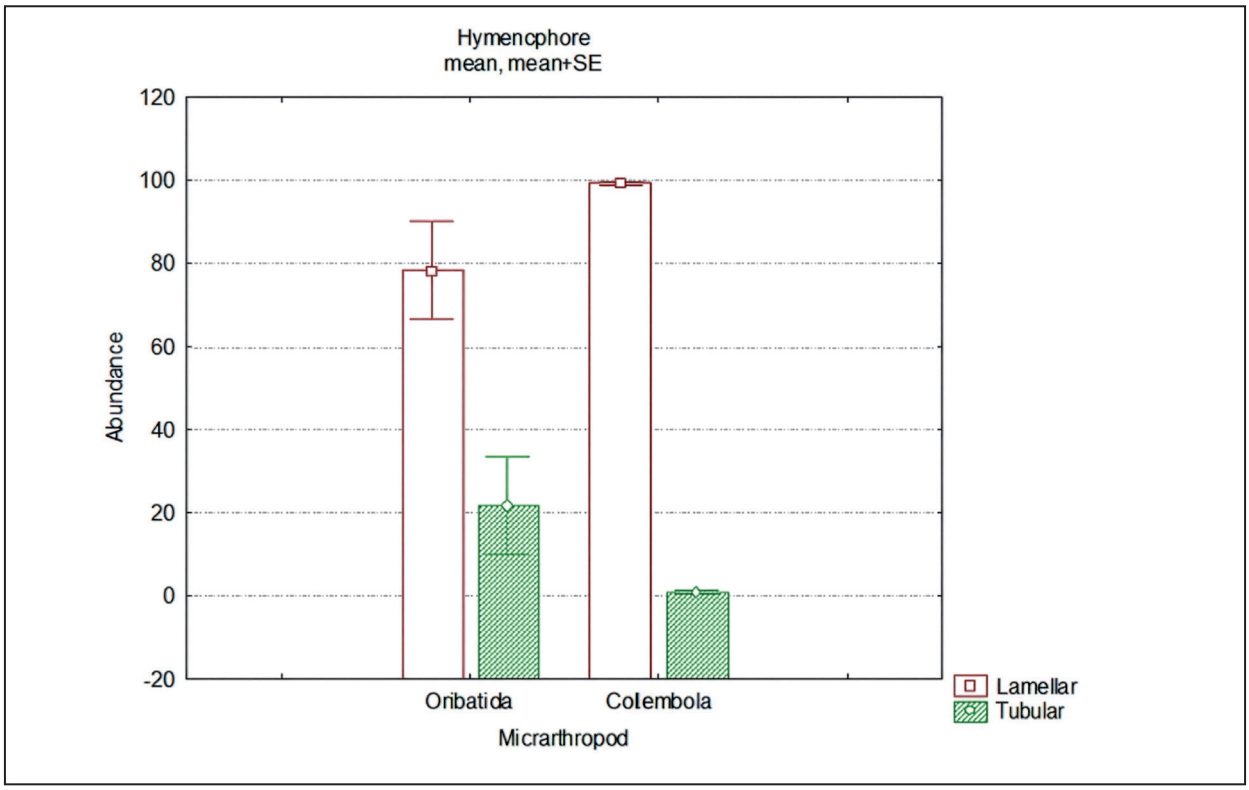

Figure 4. Abundance of Oribatida and Collembola according to mushroom hymenophore type. Abundance data are log 10 transformed, Points represent mean values. Vertical bars denote 95 % confidence intervals.

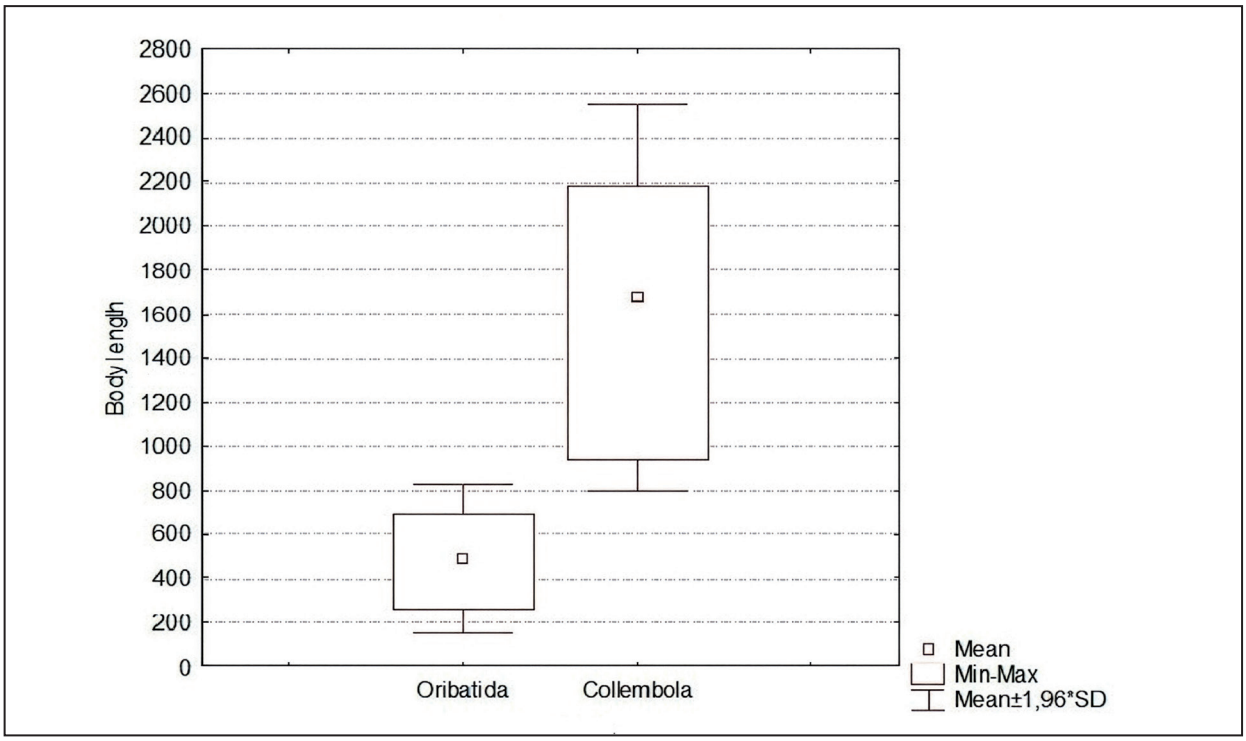

Figure 5. Body length of six most abundant Collembola and Oribatida. Min-Max: mimimum and maximum values, SD: standard deviation.

Table 4. Abundance and body size (µm) of Collembola and Oribatida associated with fungi. Data represent the **six** most abundant species from each microarthropod group.

		Lamellar	Tubular	Total
Oribatida				
Anderemaeus magellanis	**680**	**4**	**1**	**5**
Lanceoppia kovacsi	**470**	**7**	**0**	**7**
Setoppia angustopili	**700**	**12**	**0**	**12**
Membranoppia breviclava	**360**	**32**	**1**	**33**
Oppiella nova	**260**	**59**	**172**	**233**
Tyrophagus putrescentiae	**490**	**149**	**72**	**241**
Collembola				
Brachystomella parvula	**940**	**691**	**0**	**691**
Brachystomellides neuquenensis	**1950**	**857**	**0**	**857**
Ceratophysella armata	**1840**	**1194**	**38**	**1232**
Ceratophysella denticulata	**1375**	**1753**	**18**	**1803**
Entomobrya pseudodecora	**2180**	**14931**	**0**	**14931**
Hypogastrura manubrialis	**1780**	**42736**	**33**	**42769**

Hymenophore configuration

Mushrooms attract a significant number of arthropods, including mites (Acari) and flies (Diptera), some of which are known carriers of viruses and bacteria that can cause various diseases. Additionally, they may also trigger allergic reactions.

This study focused primarily on microarthropods, given the vast diversity of arthropods at smaller body sizes. Our findings indicate that hymenophores structured significantly accessibility and colonization by arthropods. Lamellar hymenophores are more accessible to larger taxa such as Diptera and Collembola, while tubular structures may offer refuges for Acari. Lamellar hymenophores, with their more open structure, tend to attract a wider range of microarthropods, while tubular hymenophores, with their smaller cavities, primarily allow the entry of very small microarthropods as Acari. This study statistically corroborated the greater abundance of Acari in tubular mushrooms compared to other microarthropods, highlighting how the structural differences between hymenophores influence the diversity of arthropod visitors. This was also evident for Diptera which have larger body maggots showing higher richness and diversity on lamellar mushrooms.

Collembola frequently colonize lamellar hymenophores in high densities, whereas smaller Oribatida, such as *Oppiella nova*, are capable of inhabiting tubular hymenophores (Tab. 4). This pattern appears to be driven by body size differences, as Oribatida are generally smaller than Collembola (Tab. 4). The ability of *O. nova*, a cosmopolitan Oribatid mite, to occupy tubular structures underscores the role of body size in determining arthropod access to hymenophore morphology. Our results therefore reinforce the hypothesis that hymenophore architecture acts as a selective filter, with accessibility being determined by arthropod body size.

Fungal toxicity and edibility

Collembolans are the most abundant insects found on edible agaric mushrooms (Yamashita & Hijii 2003) this is consistent with our study where high numbers of Collembola were found on *Agaricus arvensis* but also other edible mushroom follow the same pattern as was seen in the PCA (A. augustus and R. roseolus). It has been observed that Collembola tend to avoid fungal species toxic to humans (Shaw, 1988). Consistent with this pattern, yet contrary to our second hypothesis, the toxic *A. muscaria* supports an unexpectedly high microarthropod richness but lower abundance of Collembola. This suggests that toxicity to humans may limit, rather than entirely prevent, colonization by

certain Collembola species. Arthropods have a greater capacity for resource exploitation than humans, as they can safely consume mushrooms toxic to us. This study demonstrates that microarthropods do not exhibit distinct food preferences among the 20 mushroom species analyzed. No significant differences were observed in the abundance of Collembola and Acari, or in overall microarthropod richness, between edible and inedible mushrooms usually known as toadstools, indicating a lack of preference related to mushroom edibility. In contrast, the higher abundance of Diptera suggests a clear preference for inedible mushrooms, which aligns with their typical association with unpalatable, decomposing organic matter. This finding supports the hypothesis that access to resources with lower competition, such as toxic mushrooms, may facilitate the continued association of generalist Diptera with these substrates (Kropelin & Scott Chialvo 2024). Like Diptera, Acari also thrive in unpleasant, degrading organic matter. Their high richness and diversity on inedible mushrooms may be further increased by the presence of accompanying predators, such as certain Trombidiformes and Mesostigmata mites. The greater richness and diversity of Acari on inedible and toxic mushrooms suggest long-term adaptations to nutrient-rich, decomposing substrates, as well as resilience to fungal toxins produced as defenses against predation (Künzler 2018; Xu et al. 2023). Some mite species are even capable of accumulating alkaloids (Saporito et al. 2007, Heethoff et al. 2016). This study demonstrates that a rich and varied community of microarthropods can flourish across different mushroom species, though the structure of their hymenophore influences their growth. Platypezidae is the only family within the higher Diptera whose larvae develop exclusively in fresh fungal sporocarps, a relationship corroborated by multiple researchers (Krivosheina 2008). Consequently, the occurrence of Platypezidae is considered a reliable indicator of fresh mushrooms in the environment. However, in our study, we observed its presence exclusively in association with *Agaricus* species. This study identified 98 microarthropods species inhabiting 20 mushroom species, contributing novel insights into the microfaunal ecology of fungal substrates that, regardless of edibility, support complex arthropod communities.

Our findings align with reports from other regions where fungi sustain diverse microarthropod communities. For instance, *Polyporus betulinus* in Canada hosted a specialized fauna of mites and Collembola (Pielou & Yerma 1968), while Mexican fungi showed a high diversity of mycophilous Collembola (Palacios-Vargas & Gómez-Anaya 1994). In the Caribbean, Collembola were found feeding on fungal spores (Rosello et al. 1986). These studies confirm that fungi act as ecological hubs, supporting both common and specialized species. However, our work provides the first comprehensive documentation of such interactions in Patagonian forests, adding a biogeographically novel perspective.

The evidence presented here suggests that mushrooms play an important role in forest ecosystems by hosting abundant and diverse arthropod communities. Hymenophore structure and fungal edibility shape the accessibility and diversity of these assemblages, but toxic compounds do not necessarily deter colonization. On the contrary, toxic fungi may sustain diverse arthropod guilds, including mites with specific chemical adaptations. These findings highlight the need to consider fungal sporocarps as temporary but functionally important microhabitats within soil–litter food webs.

Given the abundance of fungi in this region, it is likely that the diversity of microarthropods associated with mushrooms is considerably high. Exploring the mesofauna of fungi thus remains a promising area for remarkable discoveries. Further research should explore seasonal dynamics, employ molecular techniques for more precise taxonomic identification, and expand investigations to include other forest ecosystems. These findings have important implications for forest biodiversity conservation and enhance our understanding of fungal–arthropod ecological networks.

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Conflict of interest statement

The authors declare that they have no conflicts of interest.

A list of species and morphospecies found can be found in the following file https://docs.google.com/spreadsheets/d/1nCrwxnxeEJT5825vaxHXcKMJCwSlb82q/edit?usp=sharing&ouid=101728083132555528549&rtpof=true&sd=true

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