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Small mammal mycophagy in hemiboreal forest communities of Lithuania

Research Article

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Abstract: The diets of small mammals in different hemiboreal spruce-dominated, oak-dominated and mixed forests in western part of Lithuania were studied by examination of fungal spores in fresh fecal pellets of caught animals. In the diets of mice (*Apodemus* spp.), bank voles (*Myodes glareolus*), and common and pygmy shrews (*Sorex araneus* and *S. minutus*), 22 different fungal taxa were identified, 15 of which were hypogeous fungi. The sporocarp abundance and the spores in fecal samples of *Elaphomyces* fungi prevailed in study area during this investigation. Although most of the captured individuals consumed fungi, the consumption varied among small mammal species. The data show that the fungi were more frequent and taxonomically diverse in *Myodes glareolus* than in *Apodemus* spp. diets. The study provided evidence that the fungal component in the diets of insectivorous *Sorex* species is more diverse than previously known. The availability of sporocarps and the fungal component in the diets of small mammals showed seasonal effects. Annual hypogeous and epigeous sporocarp abundances did not vary significantly across forest types. The significant difference in mycophagy was observed across all forest cover types, with the greatest fungal diversity in fecal samples collected in mixed coniferous-deciduous tree stands.

Keywords: *Fungal diversity • Myodes • Apodemus • Sorex • Diet*

1. Introduction

The interactions among mycorrhizal fungi, plants and small mammals are important to ecosystem processes and have been reviewed on several occasions [1-5]. Mycorrhizal fungi supply water and nutrients to the plants, and the plant roots in turn provide carbohydrates from photosynthesis to the fungi [6]. Ectomycorrhizal hypogeous fungi form below-ground sporocarps, so they rely on mycophagous animals for spore dispersal [3]. Although the digestible energy content of hypogeous fungi is lower compared with that of seeds and other foodstuff, for some small mammals the hypogeous sporocarps could be a main dietary source [3,7-9]. Consumed spores remain viable after the passage through the mammal gut and could successfully inoculate the roots of mycorrhizal plants. Ingestion of the spores by small mammals has been suggested as necessary requirement for spore germination [10]. Mycophagous mammals disperse fungal spores in forested and nonforested habitats [11] and are important prey to many predators. The mammal-fungus-tree and predator-prey relationships can be disrupted when humans manipulate forests for timber production [2,12].

Various forest small mammal species are mycophagists, and to a certain extent consume both hypogeous and epigeous fungal sporocarps. Some species in the *Sciuridae*, *Geomyidae*, *Cricetidae*, and *Phalangeridae* families rely on sporocarps for a substantial portion of their diet [4]. Other small mammals feed on fungi only occasionally. Studies of various aspects of mycophagy by mammals have been more extensive in North America and Australia, whereas the data on small mammal mycophagy in European forested ecosystems are rather limited [7]. Recent studies have been conducted into the consumption

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and dispersal of hypogeous and epigeous fungi by *Sciurus vulgaris* in the subalpine conifer forests of western Italian Alps [13].

Key areas for future research on sporocarp mycophagy include describing the feeding habits among poorly studied animal species and examining patterns of foraging and fungal resource use in space and time among diverse communities of mycophagous mammals [7]. Bank voles (*Myodes glareolus*) and yellow-necked mice (*Apodemus flavicollis*) usually inhabit deciduous and mixed-deciduous forests throughout Europe and are the dominant *Cricetidae* and *Muridae* rodent species in Lithuanian forests [14]. Little is known about the mycophagy of these mammals in European forests, especially in the hemiboreal and boreal forests of the Baltic and Fennoscandian regions. The diets of *M. glareolus* and *A. flavicollis* have been investigated in high and low-elevation forests of Bavaria in Germany [15], and the *Myodes glareolus* diet has been studied in Finland [16]. The mycophagy of insectivorous animals, e.g. shrews of the genus *Sorex*, is still poorly understood as well. Consumption of fungi by these insectivores is known only from studies originating in North America [3,17]. The mycophagy of *Sorex* animals has not been reported on in Europe.

The purpose of our study was to examine the patterns in mycophagy of forest-dwelling small mammals living in hemiboreal forest communities in the western part of Lithuania. The tasks of this investigation were to determine the composition, abundance and seasonal variation of hypogeous and epigeous fungi in the diets of animals from different genera (*Apodemus*, *Myodes*, *Sorex*), and to detect the interactions of the abundance of mycorrhizal fungi with small mammal mycophagy in spruce-dominated, oak-dominated and mixed forests.

2. Experimental Procedures

2.1 Study sites

The study was carried out between 2005-2007 in different forest communities in Žemaitija National Park in western Lithuania. The study area is situated in the hemiboreal vegetation zone. Forest cover comprises 45% of the whole park territory. Most of the forests (47%) are dominated by Norway spruce, the less common forests are those dominated by Scotch pine (26%) and dominated by birch (14%). The study area has a temperate climate, a multi-annual average rainfall

	Study plots	1	2	3	4	5
	Geographical coordinates	56°00'11,7''N 21°52'11,2''E	56°00'21,2''N 21°52'40,2''E	56°03'06,1''N 21°49'50,4''E	56°02'06,4''N 21°46'27,8''E	56°02'00,0''N 21°46'59,1''E
	Protection status	Strict nature reserve	Strict nature reserve	Landscape reserve	Landscape reserve	Landscape reserve
	Forest cover type	Spruce	Spruce	Spruce	Oak	Mixed
	Overstory species*	PIAB (4), PISY (r)	PIAB (4), PISY (+)	PIAB (4)	QURO (2), TICO (+), ACPL (+), BEPE (+), POTR (+), CABE (+)	QURO (2), PIAB (2), BEPE (2), POTR (+)
	Age of dominating trees (years)	85	95	70	108	117
	Canopy closure (%)	50	75	50	70	90
	Bush cover (%)	10	3	5	20	15
	Grass cover (%)	50	15	50	5	60
	Moss cover (%)	70	80	70	20	10
	Coarse wood debris (% cover)	5	30	5	11	15
Soil parameters	N_{total} (%)	0.159	0.48	0.399	0.37	0.492
Soil parameters	$P_2O_{5\ mobile}$ (mg/kg)	13.6	42.2	15.8	10.2	18.3
Soil parameters	$K_2O_{\ mobile}$ (mg/kg)	52.5	159	110.1	72.5	163.3
Soil parameters	Humus (%)	6.57	18.2	7.42	8.98	9.66
Soil parameters	pH_{KCL}	2.94	2.84	3.46	3.16	3.73
Soil parameters	Disturbed floor by wild boar	+	+	–	–	–

Table 1. Environmental attributes of the five study plots.

** – major tree species: ACPL – Acer platanoides, BEPE – Betula pendula, CABE – Carpinus betula, PIAB – Picea abies, PISY – Pinus sylvestris, QURO – Quercus robur, POTR – Populus tremula, TICO – Tilia cordata. Braun-Blanquet [47] cover abundance scale: 5 = >75%; 4 = 50–75%; 3 = 25–50%; 2 = 5–25%; numerous, but <5% cover; + = few, small cover; r = solitary, small cover.*

of 788 mm, a multi-annual average of temperature of 5.9°C, and a growing season length of 187 days [18].

Within the forest communities, which differ in environment and forest composition (Table 1), five permanent rectangular study plots (each 1000 m^2 in size) were established for the live-trapping of small mammals and collection of both hypogeous and epigeous fungal sporocarps. Study sites were situated an average of 9 km apart.

2.2 Sampling of fungal sporocarps

The availability of both the epigeous and hypogeous mycorrhizal fungal sporocarps was evaluated in all study plots. Epigeous sporocarps were counted during the peak fruiting time in our region in summer (August) and autumn (September-October) every three weeks during 2005–2007. Each study plot was assessed 14 times. The fructification of epigeous mycorrhizal fungi was searched for, but not observed in spring (March-May). In the field facility or laboratory, the sporocarps were identified by species. Identified species were classified into the orders *Agaricales, Boletales, Cantharellales* and *Russulales* following taxonomical arrangement of taxa provided in the *Dictionary of the Fungi* [19].

The search of hypogeous sporocarps was performed in March (2006–2007) and August–November (2005–2007) by raking with a garden cultivator the uppermost soil layer of 4 m² size temporal plots established along the outside border of each permanent plot. We avoided sampling in the same place during consecutive visits. Each study site was visited 19 times, yielding a total sample area of 76 m² in each study site. Collected sporocarps were counted and identified by species. Epigeous and hypogeous fungi were identified according to various mycological publications [20-27]. The number of counted epigeous and hypogeous sporocarps for the result analysis was converted to a per-hectare abundance of crop availability.

2.3 Sampling of small mammals

Small mammals were captured using Longworth traps. Within each plot 13 traps were placed at *ca.* 5 m intervals. Each trap was baited with a mixture of rolled oats and sunflower seeds. Trappings were undertaken as a series of 20 field trips between September 2005 and October 2007 during different seasons: in spring (March–May), summer (June–July) and autumn (September–October). During each trapping month the five plots were each trapped for one night. Total number of trap nights was 1300 (260 trap nights per plot).

Identification of captured small mammals was based on their external characteristics as in Prūsaitė [14]. Two quite similar species, namely *Apodemus flavicollis* (Melchior) and *A. uralensis* (Pallas), were found in the study area [28,29]. Field identification of *A. flavicollis* and other related species, e.g. *A. sylvaticus* L. and *A. uralensis*, is problematic [30-33], so the mammals of the genus *Apodemus* were identified only by genus. It is worth mentioning, that most of the mice caught during this study could likely be *A. flavicollis*, because rather few *A. uralensis* have been captured in Lithuanian forests [29]. Identified animals were released at the point of capture.

2.4 Diet analysis

The diets of mycophagous animals were studied by fecal pellet analysis, which can provide an accurate record of an animal's recent diet [2,3,11,12]. Fresh fecal pellets of captured animals were collected and immediately placed in vials containing 1 ml 10% formalin. A total of 131 samples of small mammal excrements were collected.

For the laboratory analysis of each individual fecal sample, we macerated the pellets and placed 2 droplets of the resulting solution and a drop of Melzer's reagent on each of 3 glass slides, and eventually covered the microscopical samples with cover slips. For each of the 3 slides, 25 systematically selected non-overlapping fields of view (5 rows of 5 fields each) were examined at 400× magnification under a compound microscope, resulting in total of 75 fields of view per individual fecal sample. The spores of hypogeous fungi were identified as in Castellano *et al*. [34] and Pegler *et al*. [27]. Detailed morphological descriptions, illustrations and taxonomical determinations of observed fungal spores are presented in the publication of Kataržytė and Kutorga [35]. The frequency of fungal taxa was calculated as the proportion of fecal samples containing the spores of a particular taxon from all examined fecal samples of a particular mammal. The relative frequency of a fungal taxon was calculated as the proportion of taxon frequency from a total frequencies of all taxa (frequency/Σ frequencies).

Spore abundance of the fungal taxon was estimated in fecal samples of each small mammal using 5 score scale: 0 – the pellet sample contained no spores; 1 – a small amount of spores (spores found in <25% fields of view); 2 – a moderate amount of spores (25–50%); 3 – a large amount of spores (50–75%); 4 – very large amount of spores (>75%).

Study reference material was deposited in the Herbarium of Vilnius University (WI).

2.5 Statistical analysis

Spore abundance was used for counting the Shannon diversity index (H′) [36]. The Kruskal-Wallis (H), Pearson chi-square and Fisher's exact tests were performed for

comparison of different variables. Comparison of the fungal composition and abundance in small mammal fecal pellets in different study plots was carried out using Bray-Curtis Similarity index (BCI) analysis [36].

3. Results

3.1 Species richness and sporocarp abundance

In total 85 mycorrhizal species (79 epigeous and 6 hypogeous) belonging to the *Ascomycota*, *Basidiomycota* and *Glomeromycota* were identified. Species richness ranged from 24 to 39 species among individual study plots (Table 2).

Annual sporocarp abundance of different epigeous and hypogeous fungal taxa significantly varied (Kruskal-Wallis H=17.614; d.f.=8; P=0.024). Six fungal groups (*Elaphomyces*, *Russulales*, *Boletales*, *Agaricales*, *Tuber* and *Endogone*) were important in respect of sporocarp availability to the mycophagy (Figure 1).

The number of fungal taxa significantly increased from spring to autumn (spring mean ± s.d.= 0.2±0.42; summer = 5.13±2.47; autumn = 17.53±4.95) (H=33.543; d.f.=2; P=0.000). The seasonal sporocarp abundancies were different in spring (mean ± s.e.= 2500 ± 500), summer (791±207) and autumn (6799±1792), and varied significantly (Kruskal-Wallis H=6.250; d.f.=2; P=0.044).

The number of fungal taxa in different study plots was similar (Kruskal-Wallis H=7.812; d.f.=4; P=0.099). Dominant abundance of the *Elaphomyces* fungi was recorded in *Picea abies* dominated stands, *Russulales* – in *Quercus robur* dominated stand and *Tuber* – in mixed forest. The sporocarp abundancies of different fungal taxonomical groups varied significantly within individual study plots (Table 2), although the variation of total epigeous and epigeous sporocarp abundancies across forest cover types was not significant (Kruskal-Wallis H=0.21; d.f.=1; P=0.885).

3.2 Animals diets

In total, 22 genera or groups of fungi belonging to *Ascomycota*, *Basidiomycota* and *Glomeromycota* were identified in 131 small mammal fecal samples (Table 3). Mycorrhizal fungi (hypogeous taxa, *Russulales*, *Boletales*) were recorded in 98 (74.8%) fecal samples, while presumably not mycorrhizal fungi were observed in 42 (32.1%) fecal samples. The spores of hypogeous and epigeous fungi were observed, respectively in 109 (83.2%) and 78 (59.5%) samples. Fifteen taxa from 9 genera represented hypogeous ascomycetes (56.9%), glomeromycetes (29.3%) and basidiomycetes (13.8%).

The spores of hypogeous *Elaphomyces* spp. and *Endogone* sp. 1 prevailed in fecal samples (Table 3).

Overall, 58 individuals of *Apodemus* spp., 67 of *Myodes glareolus*, 4 of *Sorex araneus* and 2 of *S. minutus* were captured in all study plots (Table 4). Most individual small mammals (more than 66%) consumed fungi. Various fungal microstructures (spores,

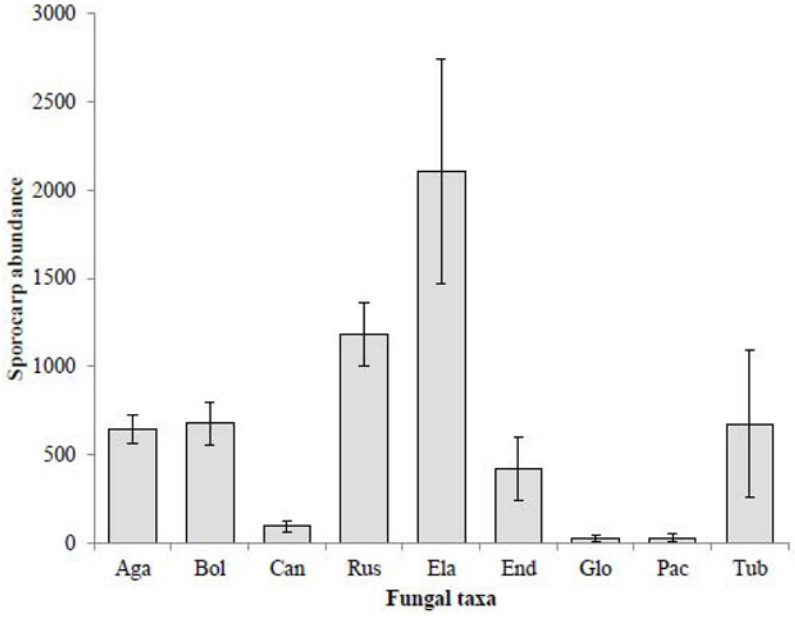

Figure 1. Sporocarp abundance (mean (±1 SE) number of sporocarps per ha) of fungal taxa sampled in 2005-2007. Epigeous fungi: Aga – *Agaricales*, Bol – *Boletales*, Can – *Cantharellales*, Rus – *Russulales*; hypogeous fungi: Ela – *Elaphomyces*, End – *Endogone*, Glo – *Glomus*, Pac – *Pachyphloeus*, Tub – *Tuber*.

		Study plot				
		1	2	3	4	5
Epigeous fungi	*Agaricales*	687 (198)	833 (267)	933 (355)	260 (84)	497 (120)
	Boletales	1130 (370)	837 (203)	790 (229)	27 (13)	600 (231)
	Cantharellales	113 (66)	183 (123)	80 (80)	-	83 (43)
	Russulales	903 (24)	1153 (15)	890 (275)	1237 (690)	1717 (241)
Hypogeous fungi	*Elaphomyces*	1349 (963)	2758 (130)	5040 (3150)	496 (312)	893 (294)
	Endogone	-	556 (367)	1250 (722)	-	278 (278)
	Glomus	-	-	-	119 (119)	-
	Pachyphloeus	-	-	-	-	139 (139)
	Tuber	833 (833)	-	-	-	2540 (1726)
	P	0.035	0.005	0.04	0.025	0.047
Total epigeous fungi		2833 (506)	3007 (385)	2693 (628)	1523 (741)	2897 (289)
Total hypogeous fungi		2183 (1092)	3313 (258)	6290 (3629)	615 (424)	3849 (2188)
Spring		500 (500)	3333 (3333)	-	-	-
Summer		210 (105)	250 (104)	290 (95)	473 (385)	473 (385)
Autumn		4915 (1044)	7131 (1082)	12195 (5814)	2091 (854)	7663 (3536)
No. of species		37	31	31	24	39
epigeous		35	29	29	22	34
hypogeous		2	2	2	2	5

Table 2. Species richness and sporocarp abundance (mean (±1SE) number sporocarps per hectare and per year) of hypogeous and epigeous fungi in study plots. P values from Kruskal-Wallis.

Taxa	Study plots					Frequency	Relative frequency
	1	2	3	4	5		
Mycelial fragments	+	+	+	+	+	71	23.5
Elaphomyces spp.[h]	+	+	+	+	+	37.4	12.4
Endogone sp. 1[h]	+	+	+	+	+	22.9	7.6
Ascomycota spp. (anamorphs)	+	+	+	+	+	18.3	6.1
Boletales spp.	+	+	+	+	+	17.6	5.8
Pachyphloeus spp.[h]	+	+	+	+	+	17.6	5.8
Genea spp.[h]	+	+		+	+	15.3	5.1
Chamonixia caespitosa[h]	+	+	+		+	14.5	4.8
Russulales spp.	+	+	+	+	+	13	4.3
Glomus sp. 3[h]	+	+	+	+	+	11.5	3.8
Tuber spp.[h]	+	+	+		+	10.7	3.5
Pezizales spp.	+	+	+	+	+	9.2	3
Endogone sp. 2[h]	+	+	+	+		6.1	2.0
Hydnotrya sp.[h]	+	+				6.1	2.0
Hymenogaster sp. 2[h]		+		+	+	6.1	2.0
Genea sp. 1[h]		+	+		+	5.3	1.8
Glomus sp. 1[h]		+	+	+	+	5.3	1.8
Fungi spp.		+			+	3.8	1.3
Glomus sp. 2[h]		+		+	+	3.1	1.0
Hymenogaster sp. 1[h]			+	+	+	2.3	0.8
Tuber sp. 1[h]			+		+	2.3	0.8
Unidentified sp. 1				+		1.5	0.5
Unidentified sp. 2		+				0.8	0.3
Total number of taxa	13	19	15	15	18		

Table 3. Fungal taxa found in small mammal fecal pellets collected in study plots, frequencies (%) and relative frequencies (%) of fungal taxa in fecal pellets; h – hypogeous fungi. Numbers specify the different taxon/species.

cystidioles, hyphae, fragments of tissue) were detected more frequently in *M. glareolus* than in *Apodemus* spp. excrements. Fungal spores were not observed in 38% of *Apodemus* spp. and in 6% of *M. glareolus* fecal samples.

The greatest number of fungal taxa (22) were detected in fecal pellets of *M. glareolus*, the lowest (4 taxa) – of *Sorex araneus*. It should be noted that only six *Sorex* individuals were caught, therefore the data on the diet of these mammals could be unrepresentative. Spores of *Elaphomyces*, *Ascomycota* spp. (anamorphs), *Pachyphloeus* and *Endogone* were the most frequent in *Apodemus* spp. excrements. Fungi of *Elaphomyces*, *Endogone*, *Genea*, *Glomus* and *Boletales* were dominant food items in the diets of *M. glareolus* (Table 4).

Diversity of all fungal taxa (Kruskal-Wallis H=34.6; d.f.=3; P<0.001) and of hypogeous taxa separately (H=30.5; d.f.=3; P<0.001) differed significantly in the fecal pellets of various small mammal taxa. The greatest value of the Shannon diversity index of all fungal taxa was in the fecal pellets of *Sorex minutus* (mean H′ ± s.d. =1.42±0.75) and *Myodes glareolus* (0.932±0.537), the smallest in the fecal pellets of *S. araneus* (0.42±0.467) and *Apodemus* spp. (0.341±0.467). Averages of hypogeous fungi diversity indices were smaller in the fecal pellets of both *M. glareolus* (0.615±0.527) and *Apodemus* spp. (0.170±0.333).

The most similar mycobiotas of fecal pellets were in *Myodes glareolus* and *Apodemus* spp. pair (BCI=54.2%), and *Sorex araneus* and *S. minutus* pair (BCI=53.8%), the least similar – in the fecal pellets of *Apodemus* spp. and *S. minutus* (BCI=28.4%).

Fungal taxa	Taxa of small mammals (n – number of captured individuals; number of fecal pellets without fungal spores)			
	Apodemus spp. (n=58; 22)	*Myodes glareolus* (n=67; 4)	*Sorex araneus* (n=4; 1)	*Sorex minutus* (n=2; 0)
Ascomycota (anamorphs)	20.7	17.9	-	-
Boletales	8.6	23.9	25	-
Chamonixia	8.6	15	50	50
Elaphomyces	24.1	49.3	75	100
Endogone	13.8	32.8	-	50
Genea	5.2	32.8	-	100
Glomus	7	28.4	-	50
Hydnotrya	-	12	-	-
Hymenogaster	1.7	15	-	-
Pachyphloeus	19	13.4	50	50
Pezizales	8.6	7.5	-	-
Russulales	5.2	20.9	-	-
Tuber	5.2	16.4	-	50

Table 4. Frequencies (%) of fungal spores in small mammal fecal pellets (unidentified fungi not evaluated).

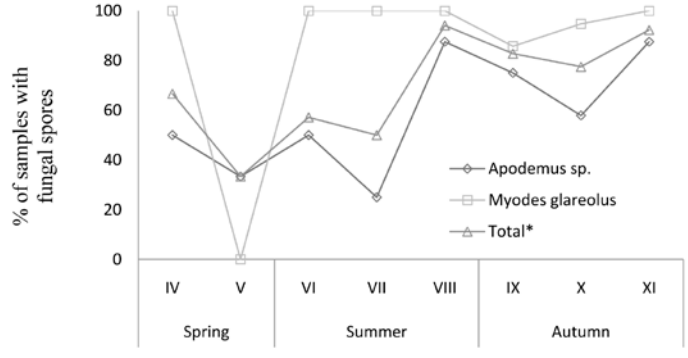

Figure 2. Proportion of small mammals pellets containing fungal spores in different seasons. * – proportion of all investigated small mammal species.

3.3 Seasonal peculiarities of mycophagy

Rodents (*Apodemus* spp., *Myodes glareolus*) consumed fungi during spring, summer and autumn (Figure 2). The number of fecal samples with fungal spores increased from spring (3 out of 6 samples, 50%) to autumn (summer 23 out of 30, 77%; autumn 79 out of 95, 83%). In different seasons the number of fungal taxa significantly (H=8.69; d.f.=2; P=0.013) varied (spring mean ± s.d.= 0.6±0.55; summer = 1.8±1.3; autumn = 2.6±1.9). Spring fecal samples contained only the *Elaphomyces* spores. The Shannon diversity index increased from spring (mean H′=0) to autumn (summer mean H′ ± s.d. = 0.52±0.63; autumn = 0.74±0.63) too (H=9.42; d.f.=2; P=0.01). The frequency of spores in fecal pellets of *Myodes glareolus* and *Apodemus* spp. was similar in summer (P>0.05, Fisher's exact test) but different in autumn (Pearson chi-square χ^2=12.8; d.f.=1; P=0).

3.4 Mycophagy in different forest communities

The numbers of all fungal taxa and as well as those of hypogeous taxa varied significantly in different forest communities (the Kruskal-Wallis test for all fungal taxa: H=11.256; d.f.=4; P=0.024; for hypogeous taxa: H=11.505; d.f.=4; P=0.014); the Shannon diversity index for all fungal taxa and hypogeous taxa varied significantly as well (the Kruskal-Wallis H=10.88; d.f.=4; P=0.03; for hypogeous taxa: H=14.15; d.f.=4; P=0.007). The greatest Shannon diversity index values of all fungal taxa (mean H′ ± s.d.= 0.94±0.65) and of hypogeous fungi (mean H′ ± s.d.= 0.75±0.56) were in mixed tree stands (plot 5).

Elaphomyces predominated in small mammal pellets collected in most forest stands, while *Endogone* was dominant in one spruce stand (Table 5). Spores of *Hydnotrya* were found only in the pellets from *Picea abies* stand.

The most similar mycobiotas in small mammal fecal pellets were found in the pair of *Picea abies* stands (plot 1 and 3) (BCI=71.4%). The least similar mycobiotas in fecal pellets were found in the pair of *Picea abies* (plot 1) and *Quercus robur* (plot 4) stands (BCI=2.9%).

4. Discussion

Mycological investigation of fresh fecal pellets from small mammals shows that in different forest communities of hemiboreal vegetation zone, rodents (*Apodemus*, *Myodes*) and insectivorous animals (*Sorex*) consume various hypogeous and epigeous fungi most intensively during summer and autumn. However, all captured small mammals are casual mycophagists, *i.e.* the animals that consume fungi during the search of other food items, or alternatively consume fungi when preferred food source is temporarily unavailable [7]. In the North-Eastern part of Europe seeds are usually the main food source for *Apodemus flavicollis*, rather than other plant material and invertebrates, while *Myodes glareolus* prefer plants, but also feed on seeds, fruits, and invertebrates [37]. The diet of *Sorex* individuals mainly consist of various invertebrates [14]. Rather limited material is published on the mycophagy of small mammals in European forest communities. Spores of hypogeous fungi were found

Fungal taxa	Study plots (n – number of captured individuals)				
	1 (n=21)	2 (n=27)	3 (n=24)	4 (n=22)	5 (n=37)
Elaphomyces	28.6	40.7	37.5	45.4	35.1
Endogone	28.6	48.2	20.8	27.3	5.4
Pachyphloeus	9.5	29.6	4.2	31.8	13.5
Genea	14.3	29.6	4.2	13.6	32.4
Chamonixia	19	33.3	4.2	–	10.8
Glomus	5	22.2	12.5	22.7	24.3
Tuber	25	11.1	16.7	–	8.1
Hydnotrya	5	25.9	–	–	–
Hymenogaster	–	3.7	4.2	13.6	16.2
Ascomycota (anamorphs)	9.5	3.7	16.7	45.5	18.9
Boletales	9.5	18.5	12.5	22.7	18.9
Russulales	5	18.5	12.5	18.2	10.8
Pezizales	5	7.4	4.2	13.6	8.1

Table 5. Frequency (%) of fungal taxa in small mammal fecal pellets collected in different study plots.

in stomach content of *Apodemus flavicollis*, *Myodes glareolus* and *Pitymys subteraneus* from Germany [15], in *Myodes glareolus* from Finnland [16], and in *Sciurus vulgaris* from Sweden and Italy [13,38]. Information about the mycophagy of insectivorous animals of the *Sorex* genus was known only from investigations from North America [3,17]. In these North American studies, only the spores of fungi from *Endogonaceae* family were recorded in *Sorex* stomach content. Therefore, the occurrence of eight fungal taxa in the pellets of *S. minutus* and *S. araneus* caught in Lithuania is of particular interest and provides additional information about the diet of these insectivores. In half of examined *Sorex* pellets we recorded both the hypogeous and epigeous fungal spores, including those of *Chamonixia caespitosa*, which is a rarely observed hypogeous basidiomycete in Europe [39]. The occurrence of fungal spores in the pellets of insectivorous animals also could be the result of the interaction between fungi, insects and animals. It is known that various invertebrates tunnel in hypogeous sporocarps to feed or lay eggs, and they could carry spores on their bodies or in their guts [5]. Individuals of *Sorex* could consume such invertebrates after they emerge or feed on hypogeous fungi.

Obtained results demonstrate that the fungi were more frequent and taxonomically diverse in *Myodes glareolus* than in *Apodemus* spp. diets. These animals predominantly consumed the fungi from the genera *Elaphomyces* and *Endogone*. In *M. glareolus* pellets the spores of *Genea* and *Glomus* were as frequent as those of *Endogone*, however, in *Apodemus* spp. pellets the frequencies of *Genea* and *Glomus* spores were much lower. The spores of *Hydnotrya* were recorded only in the excrements of *M. glareolus*. This suggests that the populations of *M. glareolus* within studied forest communities could play more an important role in the dispersal of fungal spores than the populations of *Apodemus* spp.

Annual hypogeous and epigeous sporocarp abundancies did not vary significantly across forest types. Nevertheless, hypogeous fungi predominated in the small mammal diet in all studied forest communities. Other studies have demonstrated that the spores of hypogeous fungi could predominate in the excrements or stomach contents of various animals [3,13,15]. Maser and colleagues [4] suggested that the olfactory keenness of mycophagous mammals is the main reason why the mammals looks for the fungi and enable them to locate hypogeous sporocarps precisely and dig them out with minimal waste of effort.

It is important to note that the examination of small mammal fecal pellets revealed nearly two times more hypogeous fungal genera (9 genera) in all study plots than the search of the sporocarps by raking the soil (5 genera). For example, the fungi from the genera *Chamonixia*, *Genea*, *Hydnotrya* and *Hymenogaster* were recorded only from the fecal pellets. Moreover, sporocarps of *Chamonixia caespitosa* and the genus *Genea* have not yet been found in Lithuania [40]; these hypogeous fungi are currently known in the country only from the spore material in small mammal excrements.

The sporocarp abundance and the spores in fecal samples of *Elaphomyces* fungi prevailed in the study area during this investigation. However, conflicting data have been presented in some other studies. For example, Johnson [9] reported that the sporocarps of the genus *Elaphomyces* were common in the study area but their spores were comparatively rare in the small mammal pellets. The aroma of *Elaphomyces* is rather faint comparing with other hypogeous species [9] and the digestible energy content is low compared with that of conifers seeds [8]. Moreover, *Elaphomyces* have a powdery spore mass and are likely to be discarded by small mycophagists, which focus on eating the thick peridium [7].

The spores of arbuscular endomycorrhizal fungi, particularly of the genus *Glomus*, are recorded in the excrements of ground-dwelling birds, soil- and litter-inhabiting invertebrates, and various mammals [12,41-43]. A relatively high frequency of the spores of *Glomus* was detected in small mammal pellets during our studies. We assume that the spores of non-sporocarpic arbuscular mycorrhizal fungi occurred accidentally in the pellets of small mammals during the ingestion of plant material, e.g., roots. It's also unlikely that anamorphic ascomycetes, which were recorded in studied excrements as well, constitute a beneficial food source for animals. A wide array of animals ingest fungi accidentally when foraging for other food sources [7].

Captured mammals consumed fungi during all three seasons (spring, summer, autumn). Seasonality in fungal consumption followed the seasonal availability of sporocarps, and was significant with the highest diversity occurring in autumn samples. There are only a few species of hypogeous and epigeous fungal species that produce fresh vernal sporocarps under Lithuanian climatic conditions. Therefore, it is no wonder that in spring samples we found only the spores of *Elaphomyces,* which has rather robust sporocarps that could overwinter or even start to develop early in the spring. Blaschke and Bäumler [15] also found seasonal differences in mycophagy of *Myodes glareolus* and *Apodemus flavicollis* in Germany, with a relatively small amount of spores in excrements during springtime. In subalpine conifer forests in Italy, the spring pellets of *Sciurus vulgaris* contained spores

not only of *Elaphomyces* but also of four other taxa of hypogeous fungi [13].

We assume that the diversity of hypogeous fungi found in small mammal fecal pellets in general reflects the composition of hypogeous fungi in the studied tree stands. The home ranges of the investigated small mammals are comparatively small, but they can vary in much larger ranges, depending on habitat quality, population density and animal sex. For example, the home range area of *Apodemus* species can reach up to 50000 m², and of *Myodes glareolus* can be up to a few thousand square meters [44,45]. North [46] argues that the forest types with the highest densities of truffle consumers also contain the greatest truffle abundance. This statement is nearly in accordance with the results obtained by us and zoologists during the investigations provided in Žemaitija National Park, who found that the populations of *M. glareolus* and *A. flavicollis* in Žemaitija NP are more abundant in mixed coniferous and deciduous forests than in pure spruce forests [28]. In mixed forest, we also captured a larger number of small mammal individuals and recorded the greatest diversity of hypogeous fungi in their fecal pellets. However, the observed high sporocarp abundance in this forest was not the highest among the studied forest cover types.

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