Species richness of coprophilous ascomycetes in relation to variable food intake by herbivores

Kruys, Å.[1*] and Ericson, L.[2]

[1]Department of Systematic Botany, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden
[2]Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

Kruys, Å. and Ericson, L. (2008). Species richness of coprophilous ascomycetes in relation to variable food intake by herbivores. Fungal Diversity 30: 73-81.

The aim of this study was to study species richness and species composition of coprophilous ascomycetes in boreal forest. Dung was sampled at three localities and of three herbivores; moose (*Alces alces*), mountain hare (*Lepus timidus*), and roe deer (*Capreolus capreolus*). Species richness differed significantly among dung types and we also found a significant effect of the interaction between locality and dung type on the mean number of species. The highest species richness was found on roe deer dung, while moose did not differ from mountain hare. There was a strong positive relationship between the total number of ascomycete species and the number of plant species foraged by the three herbivores. We believe that food choice is one important factor influencing the species richness of coprophilous ascomycetes, and that some species are more associated with habitat and food choice of the herbivore, rather than a specific dung type/animal species. The composition of species on the different dung types is also discussed. Our results suggest that the coprophilous mycota in the boreal forest is poorly known; we found 47 species in total, four species were undescribed, 1 was new to Sweden, 24 species were new records for the province, and we made a total of 22 new substrate records.

Key words: Ascomycota, dung inhabiting fungi, fungal ecology, species diversity

Article Information
Received 10 October 2007
Accepted 24 January 2008
Published online 31 May 2008
*Corresponding author: Å. Kruys; e-mail: asa.kruys@ebc.uu.se

Introduction

Coprophilous ascomycetes are a diverse group of saprobes including taxa from most major taxonomical groups. Some species are strictly coprophilous while others may germinate on several substrates. The coprophilous ascospores are spread by various dispersal mechanisms from the dung pile to the surrounding vegetation. The spores are often surrounded by mucilage or have gelatinous appendages, and attach easily to the plant parts on which they land (Wicklow, 1981). Feeding herbivores ingest the spores that often are darkly pigmented and well protected against both gastric juices and the harmful UV-light of the sun. With the digestive system of herbivores, spore germination can even be triggered by gastric juices (Webster, 1970).

Some species are ubiquitous, while others have high preferences for a particular dung type (Lundqvist, 1972), and dung from closely related herbivores generally have similar species composition (Richardson, 2001). This suggests that the digestive system of the herbivore may influence species composition and richness, as differences in digestion could affect both the passage of the spores through the gut, dung moisture and nutrient content. Richardson (2005) compared dung of sheep and hare that were feeding the same vegetation, and found marked differences in species compositions; differences that he attributed to differences in digestion.

Differences in ascomycete species richness and composition may also reflect differences in feeding habits and/or food choice between herbivores. Ebersohn and Eicker

(1992), in their study on African herbivores, concluded that dung from generalist herbivores feeding upon a large number of plant species was generally more diverse than dung from specialist grazers foraging narrowly within the canopy. This could, however, also be explained by a simple species/area relationship, since the generalist in their study (elephant) also has the largest dung piles.

Most previous ecological studies of coprophilous ascomycetes have been done in tropical and warm arid regions (Elshafie, 2005; Masunga *et al*. 2006; Jeamjitt *et al*. 2007), or on domesticated animals and rabbits in grasslands (Wicklow *et al*., 1980; Angel and Wicklow, 1983). Dung from wild boreal animals, and especially forest-living species, have been much less studied. The aim of this study was, therefore, to study species richness and composition of coprophilous ascomycetes on dung of moose (*Alces alces* L.), mountain hare (*Lepus timidus* L.), and roe deer (*Capreolus capreolus* L.), three common native herbivores in boreal Sweden.

During the winter season, all three animal species are browsers and forage mainly on woody plants, although at different heights. The largest component in the moose diet is pine (*Pinus silvestris* L.) and willow (*Salix* spp.), while mountain hare and especially roe deer have a more diverse diet, including more deciduous shrubs (Cederlund *et al*., 1980; Shipley *et al*., 1998; Hjältén *et al*., 2004). Moose and roe deer are ruminants, while mountain hare is a hindgut fermenter. Mountain hare cannot regurgitate the food for further mechanical breakdown, but captures the lost food content by eating faeces. Dung of mountain hare has, therefore, higher fibre content than dung from ruminants (Dorit *et al*., 1991).

Materials and methods

Study areas

Dung piles were sampled from three areas in northern Sweden; Degernäs (63°46'N, 20°13'E) and Obbola (63°44'N, 20°17'E) in the province of Västerbotten, and Nordmaling (63°34'N, 19°31'E) in the province of Ångermanland. At each site sampling took place within a 0.5 km^2 area. The three areas were selected as they all are located on the coastal plain and have vegetation mosaics characteristic for the boreal forest landscape. They also harbour large densities of the three herbivores included in the study.

Sampling

In total 87 dung piles from moose, mountain hare, and roe deer were collected in spring (23 -28th of April) 2001. The number of samples at each site were: Degernäs: moose N=10, mountain hare N=10, roe deer N=8; for Obbola; moose N=10, mountain hare N=10, roe deer N=10; and for Nordmaling: moose N=10, mountain hare N=8, roe deer N=11. Dung was collected on snow (snowpack averaged 40-50 cm), which means that it was deposited during the period December-April. Samples were placed in paper bags and brought to the laboratory.

In sampling the dung, the surface area rather than volume or weight was held constant. From each dung pile we took a sample of 55 cm^2. This equals ca. 11 pellets for mountain hare, four pellets for moose, and 25 pellets for roe deer. The area of a mountain hare pellet was estimated using the formula of a sphere ($4\pi r^2$), while the area of a moose and a roe deer pellet was estimated by using the formula for the surface area of a circular cylinder ($2\pi rh$). The volume ratios for mountain hare: roe deer: moose are 1: 1.1: 2.4, and for weight 1: 1.2: 1.7.

Dung samples were placed on filter paper in tissue culture discs and the discs were sealed with Parafilm to avoid contamination of spores between discs. The samples were sprayed with distilled water occasionally and kept at room temperature for seven months. Ascomata developing on the dung was searched on, 12th May - 20th June, and 11th - 27th November 2001. Observations were done using a stereo and compound microscope. Voucher specimens are preserved in the herbarium at Umeå University (UME), Sweden.

Nomenclature follows Eriksson *et al*. (2004) and the determinations were based on Ahmed and Cain (1972), von Arx *et al*. (1986), Bell and Mahoney (1995), van Brummelen (1967), Cain (1961), Ellis and Ellis (1998), Hansen and Knudsen (2000), Krug and Cain

(1974), Luck-Allen (1970), Luck-Allen and Cain (1975), Lundqvist (1972), and Mahoney and LaFavre (1981).

Food choice

To describe the food choice of the three herbivores in each of the three areas, data were collected on 27th-28th April 2001. We followed tracks of the different animal species at each locality and visible signs of recent foraging were noted. Foraging height (above the snow) of the three herbivores was 0-0.5 m for mountain hare, 0-1.6 m for roe deer, and 0.7-2.5 m for moose. At each locality we scored 100 bites for each herbivore and noted the species eaten.

Data analysis

Several samples were attacked by an unnatural amount of mould and bacteria during the incubation and were therefore excluded from the analyses. The complete number of samples analysed was 63 (Nordmaling; moose N = 9, mountain hare N = 5, roe deer N = 9, Degernäs; moose N = 8, mountain hare N = 7, roe deer N = 7, and Obbola; moose N = 9, mountain hare N = 9, roe deer N = 10).

We used the software R 2.1.0 for all statistical analyses (R Development Core Team, 2005). To visualize the species pool for each substrate, we performed a sample-based rarefaction curve, with resampling 10000 times (Gotelli and Colwell, 2001). To determine the effect of dung type and locality on species richness we performed a generalized linear model (GLM) with a Poisson distributed error term and a log link function (Crawley, 2002). The relationship between the species richness of ascomycetes and the number of foraged plant species was tested with a linear regression analysis. The GLM analysis was based on the species richness per sample, while the linear regression analyses were based on a pooled data set.

Results

Species richness

Fourty-seven species of ascomycetes were found in total. The cumulative species curves for the different herbivores showed a continuous increase. Roe deer increased with about one species for each new sample, while moose and mountain hare increased with one species for every second new sample (Fig. 1).

Total species richness differed between the various dung types (Table 1) and a generalized linear model revealed a significant effect of both dung type and the interaction between locality and dung type on the mean number of species per sample (Table 2). The most deviant pattern was found at Degernäs, which had both the highest (for roe deer) and the lowest mean number of species (for moose and mountain hare) found in the study (Fig. 2).

New records

We found four species, *Coniochaeta* sp., *Hypocopra* sp., *Sporormiella* sp., and *Trichodelitschia* sp. that represent undescribed species. *Sporormiella* cf. *ovina* has not previously been found in Sweden, but our specimen differs in having more cylindrical asci and smaller spores with diagonal germ-slits, compared to the original description (Nils Lundqvist, pers. comm., 2005). *Cercophora gossypina* has only been found twice in Sweden (Eriksson, 1992). Fifteen species are new to the province of Västerbotten and 17 species are new to the province of Ångermanland (Table 3). Twenty-two species represent new substrate records in Sweden; three on moose dung, five on mountain hare dung and 14 on roe deer dung (Eriksson, 1992; Hansen and Knudsen, 2000).

Substrate preferences

Only five species were abundant and found in more than 20% of the samples. The three most frequently encountered species were found on all dung types, and only one of the 11 most frequent species, *Arnium leporinum*, occurred on one single dung type, roe deer (Fig. 3). The most frequently observed species in the pooled data set was *Coniochaeta velutina*, which was found in 48% of the samples. The most abundant species differed among the various types of dung and were on: moose dung *C. velutina*, *Sporormiella vexans* and *Trichodelitschia munkii*; mountain hare dung *C. velutina* and *Podospora appendiculata*; roe deer dung *A. leporinum*,

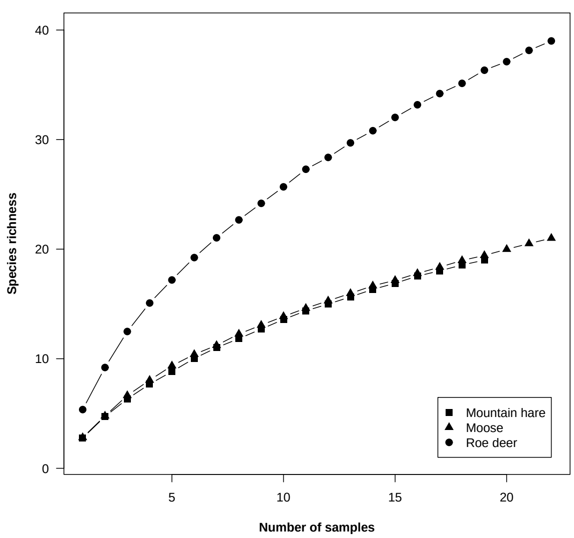

Fig. 1. A sample-based rarefaction curve of each substrate, giving an estimate of the expected number of species in the species pool.

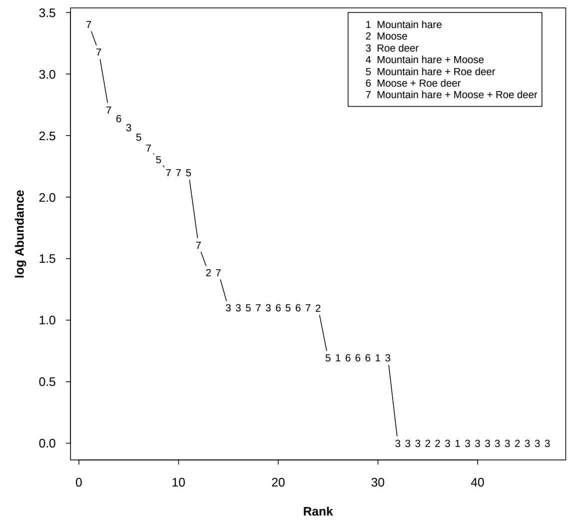

Fig. 3. A rank-abundance graph showing how the ranked ascomycete species in the pooled data set are distributed on the different dung types. The abundance values are log transformed and the species are arranged in decreasing order of abundance.

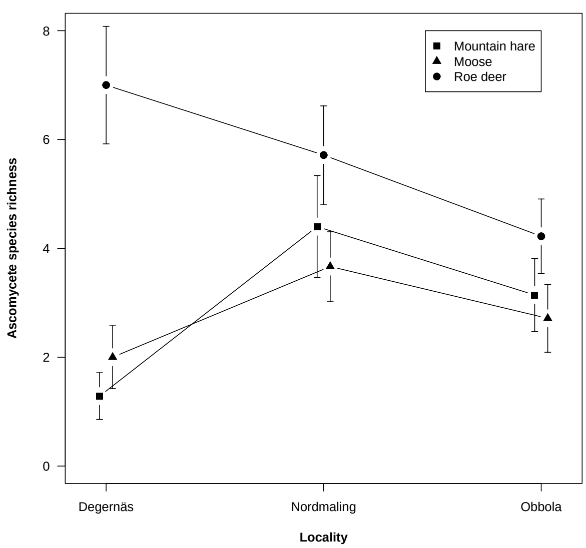

Fig. 2. The mean number of ascomycete species (± 1 SE) found on each dung type plotted against the different localities.

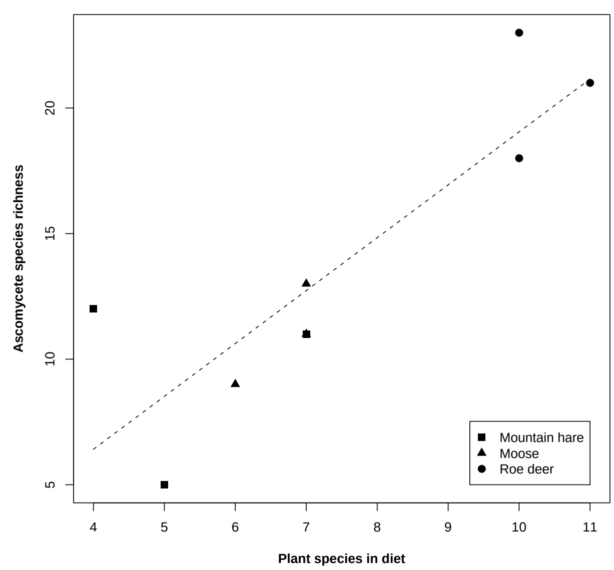

Fig. 4. The number of coprophilous ascomycetes plotted against the number of foraged plant species. The linear regression is y = 2.00x -1.796.

Ascobolus sacchariferus, *and Sporormiella* sp. (Table 3). Ten species were found on all dung types. Moose and roe deer dung shared six species, as well as mountain hare and roe deer dung. No species was associated with only mountain hare and moose dung (Fig. 3, Table 3). Twenty-five (51%) species occurred only on one substrate; five species on moose dung, three species on mountain hare dung, and 17 species on roe deer dung. The total number of species showed only a small variation between the three localities (Table 1). A large proportion of the taxa, 27 out of 47, were, however, only found in one area, eight species in Degernäs, 13 species in Nordmaling, and six species in Obbola (Table 3).

Table 1. The total number of ascomycete species found on each dung type and at each locality.

	Mountain hare	Moose	Roe deer	Total
Degernäs	5	9	20	23
Nordmaling	11	10	23	31
Obbola	11	13	16	25
Total	19	21	39	

Table 2. The results of a generalized linear model with a poisson distributed error term and a log link function, showing the effect of locality and dung type on the mean number of ascomycetes per sample. Significant p-values (< 0.05) are indicated in bold face.

	df	dev. resid.	p
Locality	2	4.76	0.092
Dung type	2	25.0	**< 0.0001**
Locality x Dung type	4	15.0	**0.005**
Residual	54	55.5	**0.005**

Species richness and food choice

The linear regression analysis revealed a statistically significant ($p < 0.05$) positive relationship between the total number of fungal species and the number of plant species in the food diet ($F_{1,7} = 18.65$, $p = 0.0035$; Table 4, Fig. 4).

Discussion

Species richness

It is important to note that although the cumulative species curves for the different dung types show that sampling was incomplete, as many as 18% of the coprophilous pyrenomycetes known from Sweden were found (Eriksson, 1992; Nils Lundqvist pers. comm.). What we sampled is only a subset of the species that one might find growing on dung and the average number of species per sample is low compared to previous studies (Richardson, 2001, 2005). This is probably a consequence of that we sampled dung deposited during winter, while most previous studies have sampled during summer, when the dung has a different consistency and is more species rich. Also, we only had the possibility to check the discs during two periods. The number of new records indicates that there are still new species to be found.

Another important result is that roe deer dung is more species rich compared to dung of moose and mountain hare in our study. A comparison with the number of coprophilous pyrenomycetes previously reported from Sweden by Eriksson (1992) on the same three substrates shows the opposite pattern, with most pyrenomycetes found on hare dung and fewest on roe deer dung. This discrepancy may be a result of that roe deer dung probably has been less studied compared to hare dung and many species therefore remain to be discovered. Also, several species reported on hare dung in Sweden have been found in the southern part of Sweden and may not grow in the north.

Substrate preferences

The comparisons between our data and earlier studies show a heterogeneous picture regarding substrate associations. We found few similarities in species composition between the two ruminants, as roedeer and moose dung shared the same number of species as roedeer and mountain hare dung. Among the 11 most frequent species only one, *A. leporinum*, was confined to a single substrate type, roe deer dung. This species has previously been considered to be associated with leporid faeces in Europe (Lundqvist, 1972; Eriksson, 1992), although Parker (1979) found it to be quite common on cervid dung in North America. A comparison between our data and Richardson (2001) indicates that six of eight shared species have the same association with either cervid or hare dung. Eight of the pyrenomycetes we found on moose and roe deer dung were listed as "associated with cervids" also by Lundqvist (1972). We found, however, only two of the 22 species listed by Lundqvist as "growing mostly on leporid dung", while another three of his "leporid species" (*A. leporinum*, *C. vagans*, *S. tetrasporum*) were in our material more frequent on moose and roe deer dung. We found eight of the 13 species that Lundqvist listed as "forest dwelling", which implies that these species are more associated with habitat and food choice of the herbivore, rather than a specific dung type/ animal species.

Table 3. Records of observed coprophilous ascomycete species at the three areas (D: Degernäs, N: Nordmaling, O: Obbola) and for different dung types (H: mountain hare, M: moose, and R: roe deer). New province records (Å: Ångermanland and V: Västerbotten) and new substrate records are based on data in Eriksson (1992), Hansen and Knudsen (2000), Lundqvist (1972, pers. comm., 2005), and Nyberg and Persson (2002).

Species	**Locality**			**Dung type**			**New records**	
	D n=19	**N n=21**	**O n=23**	**H n=19**	**M n=22**	**R n=22**	**Province**	**Dung type**
Apodospora simulans Cain & J.H. Mirza	0	4	0	0	4	0	-	-
Arnium inaequilaterale N. Lundq.	2	0	1	0	0	3	V	-
A. leporinum (Cain) N. Lundq. & J.C. Krug	4	4	5	0	0	13	V	R
A. sudermanniae N. Lundq.	0	3	0	0	0	3	Å	-
Ascobolus albidus P. Crouan & H. Crouan	0	1	1	1	0	1	-	-
A. sacchariferus Brumm.	5	3	6	0	4	10	-	-
A. michaudii Boud.	0	1	0	0	0	1	-	-
Cercophora gossypina N. Lundq.	0	2	0	2	0	0	Å	-
C. cf. *mirabilis* Fuckel	0	3	0	1	0	2	-	H
C. silvatica N. Lundq.	0	2	1	1	1	1	ÅV	-
Chaetomium elatum Kunze	0	1	0	0	0	1	Å	-
C. cf. *globosum* Kunze	1	0	0	0	0	1	V	-
Coniochaeta cf. *leucoplaca* (Berk. & Ravenel) Cain	0	3	1	1	1	2	ÅV	HMR
C. cf. *vagans* (Carestia & De Not) N. Lundq.	1	0	0	0	1	0	-	-
*C. velutina (*Fuckel) Cooke	9	9	17	15	12	8	ÅV	MR
C. sp.	0	0	5	1	2	2	V	HMR
Coprotus lacteus (Cooke & W. Phillips) Kimbr., Luck-Allen & Cain	0	0	1	0	1	0	ÅV	-
Delitschia marchalii Berl. Voglino	1	0	0	0	0	1	-	-
D. timagamensis Cain	1	0	0	1	0	0	-	-
Hypocopra sp.	1	0	0	0	0	1	-	-
Podospora appendiculata (Niessl) Niessl	1	3	5	6	1	2	Å	-
P. araneosa (Cain) Cain	0	4	6	5	0	5	ÅV	R
P. myriaspora (H. Crouan & P. Crouan) Niessl	1	0	0	0	0	1	V	-
Preussia fleischhakii (Auersw.) Cain	1	1	1	0	0	3	ÅV	-
P. funiculata (Preuss) Fuckel	2	0	1	0	2	1	V	-
Schizothecium cervinum (Cain) N. Lundq.	0	1	0	0	0	1	Å	R
S. conicum (Fuckel) N. Lundq.	0	1	0	0	0	1	-	-
S. miniglutinans (J. H. Mirza & Cain) N. Lundq.	0	1	0	0	0	1	Å	R
S. tetrasporum (G. Winter) N. Lundq.	0	0	2	0	1	1	-	-

Table 3 (continued). Records of observed coprophilous ascomycete species at the three areas (D: Degernäs, N: Nordmaling, O: Obbola) and for different dung types (H: mountain hare, M: moose, and R: roe deer). New province records (Å: Ångermanland and V: Västerbotten) and new substrate records are based on data in Eriksson (1992), Hansen and Knudsen (2000), Lundqvist (1972, pers. comm., 2005), and Nyberg and Persson (2002).

Species	**Locality**			**Dung type**			**New records**	
	D n=19	**N n=21**	**O n=23**	**H n=19**	**M n=22**	**R n=22**	**Province**	**Dung type**
S. vesticola (Berk. & Broome) N. Lundq.	2	0	0	0	1	1	-	-
Sordaria alcina N. Lundq.	2	0	0	0	1	1	V	R
S. fimicola (Desm.) Ces. & De Not.	0	0	3	2	0	1	-	-
Sporormiella australis (Speg.) S.I. Ahmed & Cain	2	5	2	1	2	6	ÅV	-
S. dubia S.I. Ahmed & Cain	0	0	1	0	1	0	-	-
S. intermedia (Auersw.) Kobayasi	1	1	1	0	1	2	-	-
S. lageniformis (Fuckel) S.I. Ahmed & Cain	1	1	1	1	1	1	-	-
S. leporina (Niessl) S.I. Ahmed & Cain	0	0	2	2	0	0	-	-
S. octomera (Auersw.) S.I. Ahmed & Cain	5	4	0	1	0	8	-	R
S. cf. *ovina* (Desm.) S.I. Ahmed & Cain	0	1	0	0	0	1	Å	R
S. tetramera S.I. Ahmed & Cain	0	1	0	0	0	1	Å	R
S. vexans (Auersw.) S.I. Ahmed & Cain	9	11	4	5	11	8	-	-
S. sp.	6	5	1	3	0	9	ÅV	HR
Thelebolus caninus (Auersw.) Jeng & J.C. Krug	2	6	7	2	5	8	-	-
T. microsporus (Berk. & Broome) Kimbr.	0	3	0	0	3	0	-	-
T. cf. *polysporus* (P. Karst.) Otani & Kanzawa	0	1	1	0	0	2	-	-
Trichodelitschia munkii N. Lundq.	2	6	3	2	6	3	-	HR
T. sp.	0	1	0	0	0	1	Å	R

Table 4. The percentage of species foraged by mountain hare (H), moose (M), and roe deer (R) at each locality. Data based on scoring of 100 bites for each herbivore and locality.

	Degernäs			Nordmaling			Obbola		
	H	**M**	**R**	**H**	**M**	**R**	**H**	**M**	**R**
Alnus incana	0	0	0	0	0	1	0	0	0
Betula pendula	0	9	2	1	21	3	0	7	7
Betula pubescens	8	14	1	8	3	0	6	3	0
Juniperus communis	0	0	4	0	0	3	0	0	4
Pinus sylvestris	0	9	0	0	2	0	0	2	3
Populus tremula	1	0	8	48	20	9	26	2	22
Salix caprea	43	2	19	10	23	20	16	10	14
Salix myrsinifolia	47	65	17	28	17	3	52	58	1
Sorbus aucuparia	0	1	3	0	14	16	0	18	44
Calluna vulgaris	1	0	1	0	0	0	0	0	0
Rubus idaeus	0	0	4	4	0	5	0	0	1
Vaccinium myrtillus	0	0	5	1	0	4	0	0	3
Graminoids	0	0	36	0	0	36	0	0	1

The differences between our findings and those of Lundqvist (1972) and Richardson (2001) is probably due to our sampling during a very limited period when foraging was mainly restricted to a narrow set of plant species, and considering the many rare ascomycete species, interpretations regarding any specificity for a certain substrate should be done with care (cf. Lundqvist, 1972).

Effects of forage

The high species richness on roe deer dung correlated to a much wider food choice by roe deer. Moose and mountain hare had the lowest number of coprophilous species at Degernäs, which was the location where these two herbivores each had the lowest diet breadth. Together, these results suggest that a more species rich diet may help explain the higher ascomycete species richness, as proposed by Ebersohn and Eicker (1992). Whether this may be a reflection of plant species diversity *per se*, or that foraging on a variety of plants ingest spores from a greater variety of fungi remains unclear, though.

The species richness and composition of coprophilous ascomycetes is of course affected by a combination of various factors in nature, like season, geographical area, dung type, and number of coprophagous insects. Based on our results and previous studies, we believe, that food choice is one important factor influencing the species richness of coprophilous ascomycetes, and that some species are more associated with habitat and food choice of the herbivore, rather than a specific dung type/ animal species.

Acknowledgements

We are grateful to Nils Lundqvist for verifying species determinations and generous information on unpublished data, and to Hans Gardfjell for statistical help. Economic support has been obtained from the JC Kempe Foundation, the Royal Swedish Academy of Sciences (Stiftelsen Th Kroks donation), and the Gunnar and Ruth Björkman Foundation.

References

Ahmed, S.I. and Cain, R.F. (1972). Revision of the genera *Sporormia* and *Sporormiella*. Canadian Journal of Botany 50: 419-477.

Arx von, J.A., Guarro, J. and Figueras, M.J. (1986). The ascomycete genus *Chaetomium*. Beihefte zur Nova Hedwigia 84: 1-162.

Angel, K. and Wicklow, D.T. (1983). Coprophilous fungal communities in semiarid to mesic grasslands. Canadian Journal of Botany 61: 594-602.

Bell, A. and Mahoney, D.P. (1995). Coprophilous fungi in New Zealand. I. *Podospora* species with swollen agglutinated perithecial hairs. Mycologia 87: 375-396.

Brummelen van, J. (1967). A world-monograph of the genera *Ascobolus* and *Saccobolus* (Ascomycetes, *Pezizales*). Persoonia, Suppl. 1: 1-260.

Cain, R.F. (1961). Studies of coprophilous ascomycetes. VII. *Preussia*. Canadian Journal of Botany 39: 1633-1666.

Cederlund, G., Ljunqvist, H., Markgren, G. and Stålfält, F. (1980). Foods of moose and roe-deer at Grimsö in central Sweden. Swedish Wildlife Research 11: 169-247.

Crawley, M.J. (2002). *Statistical computing: an introduction to data analysis using S-Plus*. Wiley, USA.

Dorit, R., Walker, W. and Barnes, R. (1991). *Zoology*. Saunders College Publishing, USA.

Ebersohn, C. and Eicker, A. (1992). Coprophilous fungal species composition and species diversity on various dung substrates of African game animals. Botanical Bulletin of Academia Sinica 33: 85-95.

Ellis, M.B. and Ellis, J.P. (1998). *Microfungi on miscellaneous substrates*. The Richmond Publishing Co. Ltd, England.

Elshafie, A.E. (2005). Coprophilous mycobiota of Oman. Mycotaxon 93: 355-357.

Eriksson, O.E. (1992). *The non-lichenized pyrenomycetes of Sweden*. SBT-förlaget, Sweden.

Eriksson, O.E., Baral, H.O., Currah, R.S., Hansen, K., Kurtzman, C.P., Rambold G. and Laessøe, T. (2004). Outline of Ascomycota-2004. Myconet 10: 1-99.

Gotelli, N.J. and Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurments and comparison of species richness. Ecology Letters 4: 379-391.

Hansen, L. and Knudsen, H. (2000). *Nordic Macromycetes vol. 1. Ascomycetes*. Nordsvamp, Denmark.

Hjältén, J., Danell, K. and Ericson, L. (2004). Hare and vole browsing preferences during winter. Acta Theriologica 49: 53-62.

Jeamjitt, O., Manoch, L., Visarathanonth, N., Chamswarng, C., Watling, R., Sharples, G.P., and Kijjoa, A. (2007). Coprophilous ascomycetes in Thailand. Mycotaxon 100:115-136.

Krug, J.C. and Cain, R.F. (1974). New species of *Hypocopra* (*Xylariaceae*). Canadian Journal of Botany 52: 809-843.

Luck-Allen, E.R. (1970). A new species of *Trichodelitschia*. Nowa Hedwigia 19: 305-309.

Luck-Allen, E.R. and Cain, R.F. (1975). Additions to the genus *Delitschia*. Canadian Journal of Botany 53: 1827-1887.

Lundqvist, N. (1972). Nordic *Sordariaceae* s. lat. Symbolae Botanicae Upsaliensis 20: 1-374.

Mahoney, D.P. and LaFavre, J.S. (1981). *Coniochaeta extramundana*, with a synopsis of other *Coniochaeta* species. Mycologia 73: 931-952.

Masunga, G.S., Andresen, Ø., Taylor, J.E., and Dhillion, S.S. (2006). Elephant dung decomposition and coprophilous fungi in two habitats of semi-arid Botswana. Mycological Research 110:1214-1226.

Nyberg, Å. and Persson, I.L. (2002). Habitat differences of coprophilous fungi on moose dung. Mycological Research 106: 1360-1366.

Parker, A.D. (1979). Associations between coprophilous ascomycetes and fecal substrates in Illinois. Mycologia 71: 1206-1214.

R Development Core Team, (2005). *R*: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org.

Richardson, M.J. (2001). Diversity and occurrence of coprophilous fungi. Mycological Research 105: 387-402.

Richardson, M.J. (2005). Coprophilous fungi from the Faroe Islands. Fródskaparrit 53: 67-81.

Shipley, L., Blomqvist, S. and Danell, K. (1998). Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. Canadian Journal of Zoology 76: 1722-1733.

Webster, J. (1970). Coprophilous fungi. Transactions of the British Mycological Society 54: 161-180.

Wicklow, D.T. (1981). The coprophilous fungal community: A mycological system for examining ecological ideas. In: *The Fungal Community*, *its Organization and Role in the Ecosystem* (eds. D. T. Wicklow and G. C. Carroll). Marcel Dekker Inc, USA: 47-76.

Wicklow, D.T., Angel, K. and Lussenhop, J. (1980). Fungal community expression in lagomorph versus ruminant feces. Mycologia 72: 1015-1021.