Diversity and occurrence of coprophilous fungi

Michael J. RICHARDSON

165 Braid Road, Edinburgh EH10 6JE, UK.
E-mail: mjrichardson@clara.net

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Fungi developing on dung samples, from a wide range of locations and incubated in moist chambers, were recorded. Highly significant differences were found among the mycobiota of different dung types, from different latitudinal ranges, and collected at different seasons. Sheep, cattle, deer, rabbit, hare and grouse provided 86 % of the 425 samples. Highly significant differences in the community composition of the mycobiota of these six dung types were observed. *Coprinus stercoreus* was the commonest basidiomycete, and most frequent on sheep, cattle, deer and rabbit; *C. miser* was the only common species, of any taxonomic group, which showed no significant difference in its frequency on different dungs. Apothecial fungi comprised about a quarter of the records, with *Ascobolus*, *Saccobolus* and *Thelebolus* spp., *Iodophanus carneus* and *Lasiobolus cuniculi* the commonest. *A. carletonii* occurred uniquely, but frequently, on grouse. Perithecial species, especially of *Schizothecium*, *Podospora*, *Coniochaeta* and *Sporormiella*, accounted for *ca* 50% of all records. The grouse dung mycobiota was markedly different, with a lower species richness (mean 3.2 per sample), from that of the mammalian herbivores, which had means of 9–12 spp. per sample. In temperate latitudes more species were recorded on samples in winter. Species richness was greater in samples from lower latitudes. Significant differences in the composition of different dung types are discussed in relation to their fungal communities. The usefulness of studying the fungi of the dung microcosm as a means of rapid biodiversity assessment is considered, by comparing the results with those of a similar, but smaller, study 30 years earlier, and by examining the diversity of a sample from a subjectively poor habitat in Morocco. There was no indication of any major change in the coprophilous mycobiota that might be associated, e.g. with climatic change or changed farming practice over the last three decades. The Moroccan samples had a much lower diversity (80 spp./50 samples) than would be expected of samples from that latitude (146 spp./50 samples) based on the worldwide data set.

INTRODUCTION

Coprophilous fungi are an important component of the ecosystem, responsible for recycling the nutrients in animal faeces, and the study of these microcosms has been advocated for the experimental study of ecosystems (Wicklow 1981). Wicklow & Moore (1974) and Yocom & Wicklow (1980) reported the results of detailed and quantitative experimental studies on the effect of environmental conditions on the coprophilous succession and community differentiation, using pellets from laboratory rabbits fed on a uniform diet of alfalfa from a single source. There have, however, been few extensive quantitative studies on the diversity and occurrence of coprophilous fungi. Wicklow (1992) noted that there are few experimental data on substrate preference, and no information on the effects of chemical composition of dung on fruiting and colonisation. Lundqvist (1972), as an introduction to his detailed taxonomic studies of the *Sordariaceae*, provided information on the preferred hosts and distribution of many species, based on a very large number (approaching 1000) of samples, mainly from Scandinavia but also from Europe and other parts of the world. He noted that although Cain (1934) and van Brummelen (1967) had also looked at large numbers of samples they had not examined the biogeography of the coprophilous mycobiota. Bell (1975) studied in detail the occurrence and development of fungi on the dung of the largely arboreal feeding brushtailed opossum, and Parker (1979) studied 163 samples of horse, cattle, sheep, rabbit, and deer collected in Illinois over 3.5 y. Other studies, more limited in scope, have been reported. Angel & Wicklow (1975) examined samples from four animal species collected from a single dry grassland locality in Colorado on a single occasion, and Angel & Wicklow (1983) examined the effects of age of dung and environment on diversity of coprophilic fungi in samples from three localities along an environmental gradient in north America. Piontelli, Santa-Maria & Caretta (1981) listed the fungi occurring on 20 samples from each of three different types of horse collected on different occasions in Chile, and Caretta, Mangiarotti & Piontelli (1994) examined 20 samples each from horse, goat and sheep dung collected from the same place on one occasion in Italy.

Lundqvist (1972) observed that all species, even those that seemed to be cosmopolitan and catholic in their requirements, showed preferences for particular dung types. He identified

three groups: (1) those with a wide ecological range and low preference for particular substrates; (2) those with a wide ecological range, but with a high preference for a particular substrate(s); and (3) fastidious species, restricted to particular substrates. He noted that the last group was relatively small, and for the Nordic *Sordariaceae*, after infrequent species (< 4 records) were omitted, included only three species from a total of *ca* 100. Lundqvist (1972) also provided lists of species which seemed to be restricted to two or three kinds of dung, often of related species, e.g. cervids, lagomorphs, rodents. Lundqvist's observations were largely supported by Richardson (1972), who reported the results of observations on 137 dung samples, mainly from the UK, and largely from cattle, sheep and rabbit. Parker (1979) also identified species that were associated with dung of particular animals, those associated with either domestic or wild animals, and those that were widespread.

It is highly likely that diversity and species occurrence will be affected by the nutritional quality of different dungs, but there is little information on dung composition. This paper reports on the fungi observed to develop on dung samples collected over five years from a variety of animals and countries, to investigate whether their occurrence could be related to or explained by dung type and chemical composition, or region and season of collection. As well as considering ecology and community structure, the results are examined to assess the usefulness of studying the dung microcosm as a means of making rapid assessments of biodiversity, since there are numerous discussions on the need to measure and monitor biodiversity, particularly in respect of concerns about climate change (e.g. Hawksworth 1994, Gaston 1996). Given the vastness of the mycobiota, the majority of which is undiscovered, the prospect of ever being able to complete an ATBI (all taxa biological inventory) is remote in any but the smallest area. Hyde & Hawksworth (1997) have considered that, for microfungi, the use of rapid biodiversity assessment methods (RBA) is not likely to be practical, because of the time necessary to train paratechnicians, even if the use of recognisable taxonomic units (RTU), rather than identification to species, is employed. To demonstrate the usefulness of a study of dung fungi for monitoring ecosystems, comparisons are made with the results of a similar but smaller study 30 years earlier, and with results from a small set of samples obtained subsequently from an apparently degraded ecosystem in Morocco.

METHODS

Dung samples

Samples of dung that appeared to be relatively recent and unweathered were collected, intermittently, from September 1994 to March 2000, into clean receptacles and usually set to incubate within a day or two of collection. If samples could not be incubated shortly after collection, they were gently air dried and stored in paper envelopes until incubation. Samples were incubated on moist filter paper or paper towelling in plastic boxes with lightly fitting transparent lids, under ambient light and at room temperature (*ca* 15–18 °C). Care was taken to ensure that cultures were not too wet. Samples were generally of similar size, with most incubation chambers 10 × 7 cm, which would accommodate approx. 2–4 g DW (= 15 sheep–24 rabbit sized pellets), or 13 × 8 cm for samples from larger animals (approx. 10–20 g DW). Samples were examined frequently at intervals of a few days, with a × 7–45 magnification stereomicroscope. Fruiting bodies were removed and mounted in water for examination at higher magnification. Samples were normally kept for 4–12 wk, with observations continuing as long as new fungi continued to be observed. Very occasionally, incubation was curtailed because of insect larval activity or heavy overgrowth with mitosporic fungi or myxomycetes. Additionally, data from 13 samples collected from Morocco in June 2000 were considered in an assessment of the use of herbivore dung samples as a means of rapidly assessing diversity. Representative and critical collections of the fungi obtained in this study have been deposited in the herbarium of the Royal Botanic Garden, Edinburgh (E).

Community analysis and species biology

The species richness of individual samples, and for all samples of each separate substrate type, was calculated using a data set comprising the 282 taxa of coprophilous ascomycetes, basidiomycetes and zygomycetes which were recorded during the study (zygomycetes, other than characteristic coprophiles which could be identified without culturing, mitosporic fungi, *Chaetomium* spp., which occurred occasionally but are not specifically coprophilous, and myxomycetes were not considered). Assessments were made of any tendency for particular coprophilous taxa to occur on dung from different animal species. Shannon's diversity and equitability (H' and E) and Sørensen's similarity (C_S) indices (Magurran 1988) were used to compare the communities on different dung types. Any seasonal differences in occurrence were simply examined by considering results from samples collected in the cooler (October–March) and warmer periods (April–September) of the year. Differences in regional occurrence were examined by comparing the frequency of occurrence of species from samples collected from different latitudinal ranges. Estimates of total species richness (S and Chao_2) were made, based on the number of species observed and the number that only occurred on one or two samples, by using the jack-knife procedure of Heltshe & Forrester (1983) and Chao (*in* Colwell & Coddington 1994):

$$S = S_{\mathrm{obs}} + ((\mathrm{n}-1)/\mathrm{n})\mathrm{L}$$
$$\mathrm{Chao}_2 = S_{\mathrm{obs}} + (\mathrm{L}^2/2\mathrm{M}),$$

where S_{obs} is the number of species observed, n = no. of samples, and L and M are the numbers of species recorded only once or twice in the sample set, respectively.

Statistical analysis

ANOVA, *t*-tests and χ^2-tests were performed as appropriate, with significant differences in ANOVA being determined by Tukey's L.S.D. or, in the case of multiple comparisons between samples of unequal size, Scheffé's L.S.D. Tests for

normality and homogeneity of variance were conducted, and consideration given to transformation, before analysis.

Cumulative species curves were constructed by plotting, in sequence, the cumulative total of species with successive samples, and fitting the curve for $y = ax^b$. In theoretical studies of species area relationships, it is usual to randomise the sample number, and often to plot the cumulative total against several separate randomisations of sample sequence to obtain the best estimate of the relationship. Since one of the points of this study has been the practical application of such a relationship to monitor ecosystems, the view has been taken that it is more useful to examine the structure of the cumulative frequency curve as it develops with successive samples as collected in the field. As a consequence, all cumulative frequencies have been plotted against sample number in the order in which they were collected.

Substrate analysis

Samples of fresh dung for chemical analysis were collected from December 1998 to August 1999. Four samples each of rabbit, sheep, deer, mountain hare, cattle and red grouse were collected from various locations in Scotland. They were gently air dried over radiators for 3–4 d, and then ground to a powder and stored for analysis. Weighed sub-samples were analysed by the Environmental Chemistry Section, Institute of Terrestrial Ecology (Merlewood, Cumbria) for total C and N, lignin, holo- and α-cellulose, starch and soluble carbohydrate content.

Nitrogen and carbon were determined using a CNS analyser (Elementar, Vario EL). Starch was estimated by extracting with deionised water and treating with 60% perchloric acid (Quarmby & Allen 1989). The amount of blue complex formed in solution with iodine was measured with a uv spectrophotometer (Pye Unicam, SP30). Soluble carbohydrates were assayed by extracting with hot deionised water, mixing with anthrone reagent and measuring with a uv spectrophotometer (Quarmby & Allen 1989). Lignin and α-cellulose were estimated after digestion of samples with dilute H_2SO_4 and wetting agent. Samples were then analysed using the ADF/H_2SO_4 gravimetric procedure in which residual fibre is treated with 72% H_2SO_4 and the final residues weighed and corrected for ash (Rowland & Roberts 1994). Holo-cellulose was estimated by extracting with acetic acid and sodium chlorite, filtering through Pyrex sintered crucibles with iced water, followed by acetone, and then ether. The final product was corrected for ash content and nitrogen expressed as crude protein (N × 6.25), even though only protein breakdown products were likely to be present. Hemicellulose (β- and γ-cellulose) was estimated as the difference between the α- and holo-cellulose values.

RESULTS

The data set analysed consisted of 4290 records from 425 samples, mostly from northern Britain (313 samples) but included some from other areas: Australia (45), mid- and southern France (32), Greek islands (11), central America (Costa Rica, Puerto Rico, Dominica and St John (USVI)) (12), Matto Grosso do Sul, Brazil (7) and the Canary Islands (Tenerife and La Gomera) (5). The majority (366) were from rabbit (*Oryctolagus*), sheep (*Ovis*), deer (*Cervidae*), hare (*Lepidus*), cattle (*Bos*) and grouse (which may have included some ptarmigan) (*Lagopus*) dung (Table 1). The commonest fungi from these 6 substrates, the most frequent 10% of species from each type, totalled 32 species, and comprised 64% of all records (Table 2, Fig. 1). At the other end of the scale, 86 species (30%) were unique. This pattern is in keeping with many studies of diversity and distribution, and reflects the situation whereby, in most communities, a relatively small number of species makes up the majority of the community, and is illustrated by the species dominance curves (Fig. 2), and the similar equitability values 0.82–0.90 of the communities on the six different dung types. Although a relatively large number of species (282) was recorded, the cumulative species curves (Figs 3, 4) show that, except for grouse dung, with a species-poor mycobiota, examination of more samples could yield many more species, since none of the other five single substrate curves, or that for the total data set, seems near to reaching the asymptote which would indicate that most species of the mycota had been observed.

Species richness and diversity

Among the six substrates that provided sufficient samples for numerical analysis there was little difference in species richness per sample, except for grouse, which had a mean of 3.2 spp. per sample, significantly fewer ($P < 0.01$, 1-way ANOVA) than the 9–12 spp. per sample for the mammalian substrates (Table 1). The overall taxonomic distribution of zygomycetes: apothecial species: perithecial (incl. pseudothecial) species: basidiomycetes was in the approximate ratio of 4:11:21:5, but there were highly significant differences in the relative proportions of these four groups on the six most frequent dung types ($\chi^2 = 191$, $P < 0.001$, 15 DF). Zygomycetes were significantly more prevalent on rabbit dung (15%), and absent from grouse. Apothecial species were more frequent on sheep and cattle (33%), and less frequent on hare (20%). Grouse and hare had relatively more perithecial species (62–67%) than other dungs with sheep the lowest (44%). *Coprinus* spp. were most frequent on ruminant dung (16–17%), compared to 8–9% occurrence on grouse and lagomorph dung.

The rabbit, sheep, deer and cattle mycobiotas were all equally diverse, with Shannon H' values of 4.1, and those of hare (3.8) and grouse (2.8) significantly less diverse (Table 1). Although there were no significant differences in species richness on the mammalian dungs, there were differences in composition of their mycobiotas. The relative frequencies of the most frequent species recorded on each of the six substrates are shown in Table 2 and Fig. 1. A dendrogram (Fig. 5) derived from the matrix of Sørensen similarity indices of these species on the different dung types (not shown) shows that the ruminant and lagomorph mycotas formed two subgroups, distinct from that of the grouse.

Table 1. No. of samples and records, mean species richness and diversity.

	Sheep	Deer	Cattle	Rabbit	Hare	Grouse
No. of samples	79	54	29	140	35	29
No. of records	939	587	334	1503	333	94
Total no. of spp.	131	108	98	154	68	27
Mean no. of spp./sample*	11.9[a]	10.9*	11.5[a]	10.7[a]	9.5[a]	3.2[b]
S.E.M.	0.45	0.63	0.83	0.34	0.74	0.45
Shannon diversity (H')	4.1[a]	4.1[a]	4.1[a]	4.1[a]	3.8[b]	2.8[c]
Species/50 samples†	97	111	149	84	92	26
Estimate of total species richness§						
$Chao_2$ (partial data set)	170	151	128	203	120	40
$Chao_2$ (complete data set)	192	161	160	278	110	55
S (partial data set)	163	138	113	169	94	38
S (complete data set)	182	148	142	219	93	40

* Mean values with the same superscript letter not significantly different ($P > 0.05$). (ANOVA after $\sqrt{(n+0.5)}$ transformation for species richness, *t*-test for Shannon H'.)

† Calculated from species-area curves ($y = ax^b$) for each dung type, solved for $x = 50$.

§ $Chao_2$ estimated from no. of species occurring once or twice only, and *S* from no. of species occurring once only (see text).

Table 2. Frequency (%) of the commonest* species on different dung types (no. of samples in brackets).

	Sheep (79)	Deer (54)	Cattle (29)	Rabbit (140)	Hare (35)	Grouse (29)
Pilaira moreaui	+	+		29	14	
Pilobolus crystallinus	46	52	21	46	14	
P. kleinii	24	13	24	11		
Ascobolus albidus	29	44	14	22	17	+
A. carletonii						41
A. furfuraceus	+	+	28	+		
A. immersus	63	20	59	+	+	+
Iodophanus carneus	52	13	55	29	+	
Lasiobolus cuniculi	24	35	14	11	+	
Ryparobius polysporus	+	+	+	22	17	
Saccobolus versicolor	38	30	17	54	23	
Thelebolus microsporus	23	11	17	+		
T. nanus	43	20		26	26	
T. stercoreus	+	13		11	51	
Coniochaeta ligniaria	10	13	14	18	49	31
C. scatigena	13	31	+	17	29	
Phomatospora coprophila	27	+	10	+		
Podospora appendiculata	+	11		+	49	
P. decipiens	53	20	62	32	14	
P. pleiospora	+	+	+	21	+	
Schizothecium conicum	49	30	66	19		+
S. tetrasporum	10	30		78	26	
S. vesticola	73	67	28	39	37	
Sordaria humana	+	11	+	+	31	+
Viennotidia fimicola	18	30		28	+	10
Sporormiella australis	24	28	17	32	91	10
S. intermedia	33	35	41	58	66	10
S. minima	16	+	31	+	+	66
Trichodelitschia bisporula	18	30	+	11	26	+
Coprinus miser	35	20	45	28	20	21
C. pellucidus	18	22	41	+		
C. stercoreus	56	61	55	51	20	+

* The 10% most frequent spp. on each of the substrates.

+ = present, < 10%; blank = not observed.

Zygomycetes

As culture methods were not used it was not practical to accurately identify most zygomycetes, and recording was limited to the characteristic coprophils that are readily observable with a stereoscopic binocular microscope. *Pilobolus* and *Pilaira* spp. were by far the most frequent fungi observed in this group, with *Pilobolus crystallinus* making up almost 36% of all zygomycete records. Eight of the eighteen species of *Pilobolus*, *Pilaira*, *Phycomyces*, *Piptocephalis* and *Chaetocladium* (the latter two both parasitic on *Mucorales*) recorded comprised 89% of the zygomycete records. The zygomycete species richness of rabbit pellets was significantly higher (1.6 per sample) than that of any of the other five substrates, which ranged from nil on grouse and an average of 0.7 per sample for the others.

Ascomycetes

This group provided by far the largest number of species, and the occurrence of apothecial and perithecial types is considered separately. Eighty-nine apothecial species in 19 genera were recorded, and the most frequent were *Saccobolus versicolor*, *Iodophanus carneus*, *Ascobolus immersus*, *Asc. albidus*, *Thelebolus nanus* and *Lasiobolus cuniculi*, together accounting for 53% of all apothecial fungi observed. Occurrence ranged from an average of 1 species per sample for grouse dung to 3.8 for sheep. Of the 152 species from 30 perithecial genera observed, ten comprised 54% of the records in the group: *Schizothecium vesticola*, *Sch. tetrasporum*, *Sch. conicum*, *Podospora decipiens*, *Sporormiella intermedia*, *Sp. australis*, *Sp. minima*, *Coniochaeta ligniaria*, *C. scatigena* and *Viennotidia fimicola*. Grouse samples had significantly fewer perithecial species (average 2 per sample) than the other substrates, which averaged 5.6 per sample, but they comprised the majority (62%) of all fungi recorded on grouse.

Basidiomycetes

The majority of agarics developing on incubation were *Coprinus* spp., and only they are considered. There was no significant difference between their occurrence on grouse and hare dung, with an average of 0.5 sp. per sample. Levels on the other 4 substrates were not significantly different from each other, and averaged 1.4 spp. per sample. *C. stercoreus* and

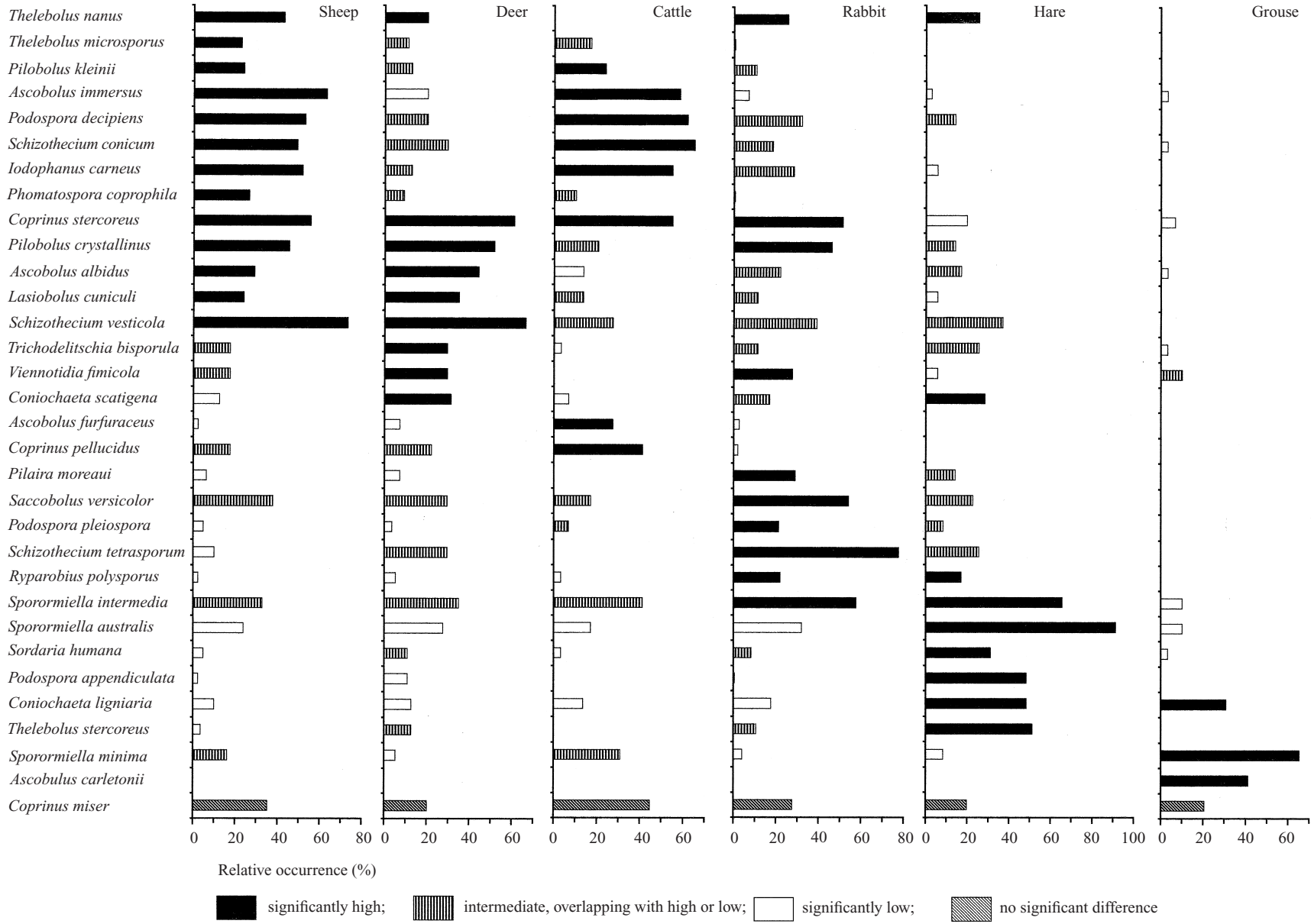

Fig. 1. Occurrence of common coprophilous fungi on different dung types. Significance levels for each species based on 1-way ANOVA, Scheffé's L.S.D. ($P = 0.05$).

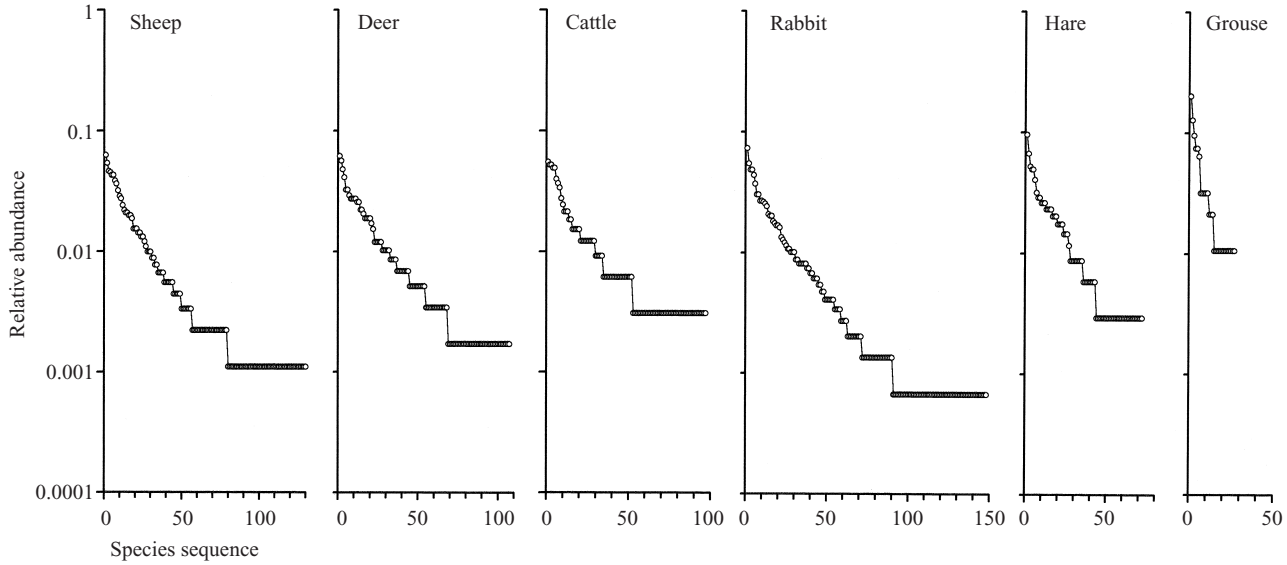

Fig. 2. Relative abundance plots of the mycobiotas of six different dung types. Relative abundance of each species is the proportion of the total number of records for each substrate. Species sequences are arranged in decreasing order of abundance. All graphs plotted to the same scale.

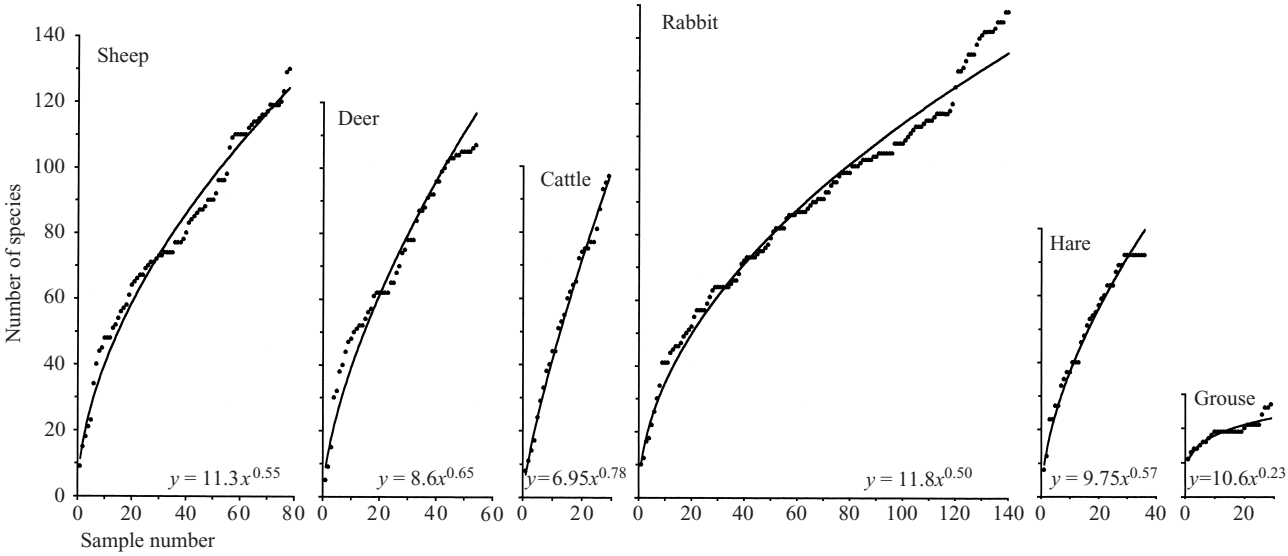

Fig. 3. Cumulative total of taxa observed in successive samples of the six most frequent dung types. Lines of best fit and equations given on the graphs ($y = ax^b$). All $R^2 > 0.9$. All graphs plotted to the same scale.

C. miser were the most frequent and widespread agarics developing on dung with incubation (44 & 27% occurrence, respectively).

Species associations

There are distinct groups of species amongst the 32 commonest species on the different dung types (Fig. 1). Of the common species, *Coprinus miser* was the only one, in any taxonomic group, which showed no particular substrate preference. *C. stercoreus* was significantly less frequent on hare and grouse dung than on the others. Grouse dung was characterised by its species-poor mycobiota, dominated by *Sp. minima* and *Asc. carletonii*. Rabbit dung was notable for its high frequency of zygomycetes, including the associated parasitic *Piptocephalis* and *Chaetocladium* spp., and abundant *Sacc. versicolor*, *Sch. tetrasporum* and *Sp. intermedia*. Hare pellets had relatively high levels of *Thelebolus stercoreus*, *Coniochaeta* spp., *Sordaria humana*, *Podospora appendiculata* and *Sporormiella* spp. Characteristic species on dung of cattle, sheep and deer, all ruminants, were similar with *Coprinus stercoreus*, *Pilobolus* and *Ascobolus* spp., *I. carneus*, *Lasiobolus cuniculi*, *Sch. conicum*, *Sch. vesticola* and *P. decipiens* prevalent and, additionally, *Viennotidia fimicola* and *Trichodelitschia bisporula* on deer, and *Coprinus pellucidus* on cattle dung.

Seasonal differences

Significantly more records were obtained from 'winter' samples (mean 11.2 species/sample, October–March) than

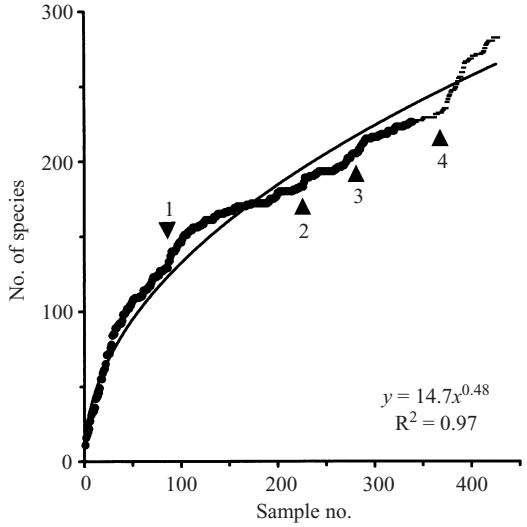

Fig. 4. Cumulative total of taxa observed in all samples. The line of best fit ($y = ax^b$) is calculated from samples 1–339 (●) (see text), extrapolated to cover the additional samples to the total of 425 (—) studied. Arrowheads indicate the start of sequences of extra-European samples: 1, Costa Rica/Puerto Rico (5 samples); 2, Puerto Rico/US Virgin Islands (6); 3, Brazil (7); and 4, Australia (45).

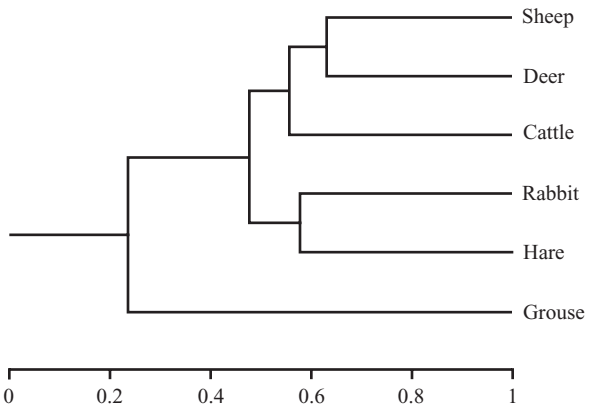

Fig. 5. Dendrogram, based on Sørensen similarity coefficients, of the relative occurrence of the 32 commonest species on different dung types.

from 'summer' (9.2 species/sample, April–September) samples ($P < 0.001$, 1-way ANOVA). The 69 samples from central and south America and Australia, where seasonal differences are likely to be smaller, or samples were only collected in one season, were omitted from the analysis. The cumulative frequency curves for 'summer' and 'winter' samples were almost identical (predicting 90 and 96 species/50 samples, respectively). Of the commoner species (Table 2) *Asc. albidus*, *Sacc. versicolor*, *Sch. tetrasporum*, *Coprinus miser* and *C. stercoreus* and the zygomycetes all occurred at significantly higher levels (χ^2 tests, $P < 0.05$), to the extent of 45–115% more, in winter samples. *Coniochaeta ligniaria* was the only species to occur significantly (2.75 ×) more frequently on summer samples (χ^2 *test*, $P < 0.01$). *Ascobolus carletonii* was more frequently observed in colder months. It occurred on all 8 'winter' samples, and on only 4 out of 21 'summer' samples, a difference which is highly significant ($\chi^2 = 15.7$, $P < 0.001$), although the expected number of observations in the winter cells of the contingency table are below the 5 considered to be necessary for a valid test. None of the other 22 species in Table 2 showed any significant seasonal differences.

Table 3. Species richness in samples from different latitudinal zones

Latitude (°) N or S*	No. of samples	Mean no. of species/sample	No. of species/50 samples†
All samples			
0–30	26	10.9	153
30–40	48	10.0	151
40–50	32	10.9	123
50–55	53	11.5	107
55–56	102	11.3	99
56–57	56	11.7	94
57–60	61	8.7	108
Rabbit			
0–45	25	10.6	120
45–55	30	11.1	95
55–56	50	9.6	96
56–60	35	10.0	93
Sheep			
0–45	18	11.1	147
45–56	39	12.5	108
56–60	22	11.5	116

* Southern Hemisphere represented only in 0–30 and 30–40° zones.
† Derived by solving the cumulative frequency curve equations for the different zones.

Latitude effects

Latitudinal gradient

To allow like to be compared with like, data from grouse were omitted from the examination of regional differences, since a comparable type of dung was not sampled outside Britain. Records from a few other atypical dungs were also omitted, e.g. carnivorous fox and canopy feeding possums. The samples from different regions, therefore, came from a similar mixture of animal types. Season of collection was confounded in the sampling, but since 'winter' and 'summer' diversity of temperate samples was similar they were not treated separately in the latitudinal analysis. Data sets were subdivided by latitude to allow as many different zones as possible to be considered with a similar number of samples in each (Table 3). As a consequence, the northerly zones are relatively narrow since more samples came from there. The species-area curves ($y = ax^b$) for each zone were used to estimate the number of species to be expected in 50 samples taken from different latitudinal zones by solving the equations for the respective zones for $x = 50$.

Species richness of the coprophilous mycobiota decreased significantly ($P < 0.01$) with increasing latitude (Table 3, Fig. 6). There was, however, no significant difference in the mean number of species observed per sample from different latitudinal zones.

Species differences with latitude

Amongst the commonest species there were many significant trends and differences in occurrence with changing latitude

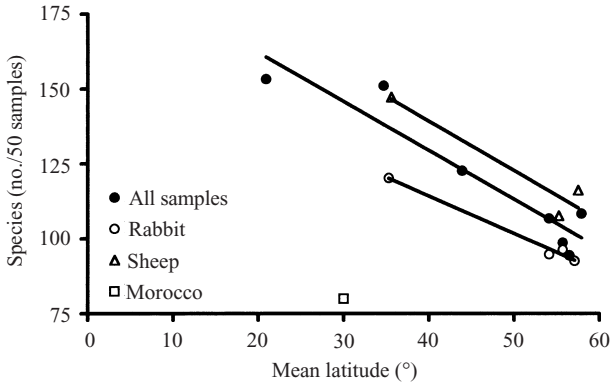

Fig. 6. Species richness of the coprophilous mycobiota of samples from different latitudes. The estimated no. of species from 50 samples was calculated from the cumulative species curves from a reduced data set (see text), and for rabbit and sheep samples, grouped in latitudinal zones to have approx. similar no. of samples in each zone. Overall latitude range 60°N–39°S (−35°S for sheep). The Moroccan value was obtained from the cumulative species curve obtained from thirteen samples subsequently collected from an apparently degraded habitat.

(Table 4). Eight species were recorded much more frequently from high latitude samples (> 50°), by a factor of *ca* 1.5–5 x, and a ninth, *Viennotidia fimicola*, was only recorded once from the 111 lower latitude samples, compared to a 23 % occurrence on samples from > 50°. Many of the commonest species showed no significant difference in occurrence with the latitude of sample collection, but *Asc. immersus*, *Sp. intermedia* and *Sp. minima* were more frequently recorded from latitudes < 45°.

Although relatively few species occurred at frequencies high enough to allow comparisons of differences, related species may share some similarities in their ecology, and useful comparisons could perhaps be made at the generic level (Table 5). Some genera were significantly more frequent in winter samples, and only *Coniochaeta*, *Podospora* and *Sphaerodes* in summer samples. *Pilobolus*, *Ascobolus*, *Thelebolus*, *Schizothecium*, *Coniochaeta* and *Coprinus* were recorded at significantly higher levels from higher latitudes (> 50°), whilst *Coprotus*, *Saccobolus*, *Sordaria*, *Podospora*, *Hypocopra* and *Sporormiella* were relatively more frequent at lower latitudes (< 45°).

Moroccan samples

The thirteen samples from Morocco (sheep, goat, ass, rabbit and camel) yielded 47 species from the same set of taxa comprising the worldwide study, with a mean of 10.8 species per sample. Many were recorded from several samples, so that the cumulative species curve was relatively shallow ($y = 14.97x^{0.427}$, *cf* Figs 3–4 for worldwide values), predicting 80 species per 50 samples (Fig. 6).

Dung chemistry

The results of dung sample analyses are given in Table 6. There were no significant differences in the amount of nitrogen in dung samples from the different animals, but different levels of total carbon resulted in significantly different C/N ratios, ranging from 22–24 in deer, cattle and rabbit, to 37 in grouse. Similarly, different lignin levels resulted in significantly different L/N ratios, from 6–10 in rabbit, cattle and hare, to 25 for grouse. Soluble carbohydrate levels were significantly higher in grouse dung, and amounts in rabbit and hare were higher than in the ruminant dungs. Starch levels were low and not significantly different. Amounts of the less readily available cellulose and lignin varied significantly among dung types, with lignin levels relatively high in deer

Table 4. Latitudinal differences in frequency (%) of species occurrence. Species arranged approximately in order of latitudinal occurrence, with higher latitude species first.

	Mean†	60°N–55°N (247)§	55°N–50°N (66)	45°N–40°S (111)
Ascobolus albidus	22	**31**	14	6
*Coniochaeta ligniaria**	18	**22**	8	14
Pilobolus crystallinus	35	**40**	**48**	14
Saccobolus versicolor	32	**36**	**38**	17
Schizothecium conicum	25	**31**	**35**	6
*S. tetrasporum**	36	**38**	**45**	25
Coprinus stercoreus	44	**47**	**64**	24
Thelebolus nanus	22	**28**	**29**	5
Viennotidia fimicola	18	**23**	**24**	1
Coprinus miser (ns)	26	28	33	19
Schizothecium vesticola (ns)	43	48	33	39
Podospora decipiens (ns)	32	29	45	29
Sporormiella australis (ns)	30	30	26	34
Lasiobolus cuniculi (ns)	17	18	14	18
Iodophanus carneus	27	23	**45**	26
Ascobolus immersus	23	18	**36**	**27**
Sporormiella intermedia	42	43	23	**50**
S. minima	16	9	9	**34**

† Overall mean % occurrence ($n = 424$).

§ No. of samples in each latitudinal range.

Differences between regions highly significant (χ^2-test, $P = < 0.02$) unless otherwise indicated. * $P < 0.05$), ns = no significant difference. High values highlighted in **bold**.

Table 5. Latitudinal and seasonal differences in frequency (mean no. of records/sample) of generic occurrence.

	60°N–55°N (247)**	55°N–50°N (66)	45°N–40°S (111)	Winter (107)	Summer (249)	W/S ratio†
Ascozonus (4)*				**[0.08]**	[0.03]	**2.99**
Phomatospora (2)	0.08	0.15	0.09	**0.16**	0.06	**2.83**
Piptocephalis (5)	0.12	**0.30**	0.02	**0.22**	0.11	**2.07**
Coprotus (14)	0.19	0.11	**0.34**	**0.28**	0.14	**1.94**
Delitschia (7)	0.11	0.06	0.16	0.17	0.09	1.82
Pilobolus (4)	**0.57**	**0.70**	0.31	**0.82**	0.46	**1.80**
Arnium (7)	0.16	0.11	0.14	0.21	0.13	1.55
Ryparobius (3)	0.11	0.11	0.15	0.15	0.10	1.55
Ascobolus (14)	**0.79**	**0.82**	0.55	**0.99**	0.67	**1.47**
Pilaira (3)	0.22	**0.35**	0.14	0.28	0.20	1.40
Viennotidia (1)	**0.23**	**0.24**	0.01	0.26	0.19	1.39
Thelebolus (6)	**0.55**	0.45	0.24	**0.63**	0.46	**1.37**
Coprinus (17)	**1.29**	**1.50**	0.94	**1.59**	1.18	**1.35**
Iodophanus (1)	0.23	**0.45**	0.26	0.31	0.23	1.32
Schizothecium (11)	**1.24**	**1.32**	0.92	**1.46**	1.11	**1.31**
Saccobolus (7)	0.41	0.50	**0.62**	0.49	0.38	1.27
Sporormiella (14)	1.08	0.73	**1.81**	1.10	1.06	1.04
Trichodelitschia (3)	0.16	0.06	0.18	0.15	0.16	0.95
Lasiobolus (4)	0.22	0.15	0.21	0.17	0.22	0.75
Sordaria (8)	0.18	0.26	**0.61**	0.22	0.31	0.72
Podospora (16)	0.55	0.77	**1.36**	0.49	**0.69**	**0.70**
Coniochaeta (8)	**0.56**	0.20	0.30	0.35	**0.52**	**0.66**
Hypocopra (8)	0.09	0.02	**0.13**	0.06	0.10	0.58
Sphaerodes (1)				0.01	**0.07**	**0.14**

* No. of species in each genus.

** No. of samples in each category.

Values in **bold** significantly higher (χ^2-test, $P < 0.05$), or different (W/S values); values in [ ] where test nearly valid ($f_e 4 < 5$); no values where χ^2-test invalid as a result of $f_e < 4$.

† Relative winter occurrence, when summer = 1.0.

Table 6. Chemical composition (%) of different dung types (mean of 4 samples).

	L.S.D.	Sheep	Deer	Cattle	Rabbit	Hare	Grouse
Nitrogen (N) (ns)*	0.8	2.0	2.3	2.2	2.2	1.9	1.6
Carbon (C)	3.9	51.3^{b}	$\mathbf{53.0}^{bc}$	46.8^{a}	47.5^{a}	$\mathbf{53.3}^{bc}$	$\mathbf{56.3}^{c}$
Starch (ns)	0.8	0.19	0.19	0.43	0.78	0.43	0.61
Carbohydrate	0.9	1.6^{a}	1.7^{a}	1.9^{ab}	2.3^{ab}	2.7^{b}	$\mathbf{4.5}^{c}$
Lignin (L)	10.8	$\mathbf{27.3}^{bc}$	$\mathbf{37.5}^{c}$	14.8^{a}	13.3^{a}	19.5^{ab}	$\mathbf{38.0}^{c}$
α-cellulose	8.2	$\mathbf{22.3}^{ab}$	19.3^{c}	$\mathbf{22.3}^{ab}$	$\mathbf{30.0}^{b}$	$\mathbf{27.0}^{b}$	20.5^{a}
Hemicellulose	5.6	30.5^{ab}	30.5^{ab}	25.3^{a}	28.8^{ab}	$\mathbf{33.3}^{bc}$	$\mathbf{38.8}^{c}$
Holo-cellulose	9.6	$\mathbf{52.8}^{ab}$	49.8^{a}	47.5^{a}	$\mathbf{58.8}^{b}$	$\mathbf{60.3}^{b}$	$\mathbf{59.3}^{b}$
C/N ratio	12.0	$\mathbf{26.1}^{ab}$	24.2^{a}	23.3^{a}	21.8^{a}	$\mathbf{27.7}^{b}$	$\mathbf{36.7}^{b}$
L/N ratio	9.5	14.1^{ab}	$\mathbf{17.3}^{c}$	7.4^{a}	6.1^{a}	10.0^{ab}	$\mathbf{24.9}^{c}$
Cellulose/lignin ratio	1.6	2.0^{ab}	1.3^{a}	3.3^{bc}	$\mathbf{4.5}^{c}$	3.4^{bc}	1.6^{a}

* ns = no significant difference; values in any row not sharing a common superscript letter are significantly different ($P < 0.05$, Tukey's Least Significant Difference test). Significantly high values are highlighted in **bold**.

and grouse dung and lowest in cattle and rabbit, and cellulose levels highest in rabbit, hare and grouse and lowest in deer.

DISCUSSSION

Diversity and community structure

Although observational rather than experimental, this study has demonstrated and confirmed the coprophilous habitat as one with a rich diversity of microfungi. The structure of the fungal community on dung follows that already well established for floras and faunas (Brown & Lomolino 1998), and for fungi (e.g. Christensen 1981, Bills & Polishook 1994). Examination of the cumulative frequency curves for species, on specific substrates (Fig. 3), and for the whole data set (Fig. 4), suggests that, even with a relatively large study, many more species might be expected with a modest increase in sample size, at least for the mammalian substrates studied. A 50% increase in sample size might be expected to yield 30–40 more species for each of the four largest sample groups (n = 35–140). Only for substrates with a restricted or fastidious mycobiota, as indicated by a markedly different form of the relative abundance plot, e.g. grouse, which has fewer dominant species and a shorter tail of low frequency species (Fig. 2), is a sample size of 30–40 adequate to discover a high proportion of the species likely to be present. The wide, shallow relative abundance plots, with long tails of species seen only once or twice (Fig. 2), of the rabbit and ungulate mycobiotas indicate

that these substrates have a far higher species richness potential, which is also shown by the high values of b in the equations for the cumulative frequency curves. On a non-log scale, curves should reach an asymptote when sampling approaches adequacy. The lines of best fit are described by the power formula $y = ax^b$ which, in another notation ($S = cA^z$), is the accepted formula for species-area and cumulative frequency curves (Rosenzweig 1995). When plotted on a log-log scale, the relationship is linear, and both a and b influence the slope of the curve. The greater the slope, the higher the species richness. By using the community structure, in particular the number of species that only occur on one or two samples, it is possible to estimate the total number of species in the habitat (*S*, Heltshe & Forrester 1983; and $Chao_2$, Chao *in* Colwell & Coddington 1994).

The usefulness of the species abundance curve to predict species richness is illustrated by the fact that the original intention was to cease sample collection at the end of 1998. The cumulative frequency curve for the 226 species derived from the 339 samples at that date indicated that a 25% increase in the number of samples could be expected to yield a further 38 species (Fig. 4). An additional 86 samples (25.4%) collected in 1999–2000 were included in the data set, and they resulted in an additional 56 species being recorded. Part of this increase can be attributed to the fact that just over half of the additional samples were from a part of the world not represented in earlier samples – mainly Australia, which included dung from marsupial herbivores, in addition to that from domesticated species. Such discontinuities in the cumulative frequency curves resulting from moves to collecting in new areas are illustrated in Fig. 4, where the first few samples from a new area coincide with a step in the cumulative frequency curve, which then continues along a similar trend to the earlier part of the line. The $Chao_2$ and *S* values obtained for the six single dung types are given in Table 1, but they give conflicting information with regard to species richness when compared to the estimates obtained from using the species-abundance curve data for the six dung types. The $Chao_2$ estimate for the whole set of samples, with 82 species occurring only once and 36 occurring only twice, out of a total 282 species, is 375 species ($S = 364$), and for the interim total of 339 samples to the end of 1998, the estimated $Chao_2$ total number of species is 292 ($S = 288$). These are relatively large changes in the estimated total value, for an addition to a relatively large number of previous samples, albeit that some of that increase was from a different area. On a single substrate basis, the $Chao_2$ values from additional sampling were all higher, except for hare dung, than when estimated using the interim data (cattle 128 → 160 [additional $n = 6$], sheep 170 → 192 [$n = 8$], deer 151 → 161 [$n = 11$], rabbit 203 → 278 [$n = 27$], hare 120 → 110 [$n = 2$], and grouse 40 → 55 [$n = 2$]), but the actual increase was more nearly predicted by the partial data set species-abundance curve equation. It would seem, therefore, that the $Chao_2$ estimate is quite sensitive to changes in sample size. The estimates of species richness from the Heltshe & Forrester formula (*S*) are generally lower (Table 1), but of the same order as $Chao_2$, with a slightly better correlation ($R^2 = 0.95$ & 0.90, respectively), between the partial and complete data sets. The

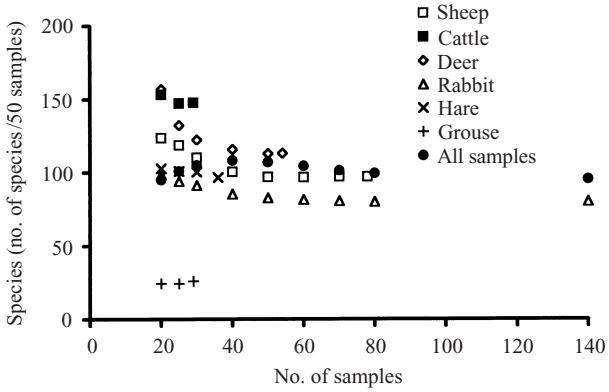

Fig. 7. Estimates of species diversity (no. of species/50 samples), with increasing number of samples, using the species-abundance curve equations for increasing numbers of samples of each dung type ($n = 20$, 25, 30, 40, 50, 60, 70, 80 and the maximum no. of samples for each dung type), and for the total data set over the same range.

use of species-abundance curve formulae to estimate species richness, in terms of species/unit no. of samples, appears, however, to be much more robust (Fig. 7). When the cumulative frequency data are used to calculate the formulae for the species-abundance curves for intermediate numbers of samples, up to the maximum collected for each dung type, the curves become asymptotic at about the 40–50 sample level. More studies are needed to see whether jack-knife or $Chao_2$ provide better estimates of diversity and species richness than extrapolation of species abundance curves. Both methods are simple to compute but, if *S* and $Chao_2$ are as sensitive to sample size as this study suggests, it may be preferable to obtain an estimate of species richness per *N* samples, as advocated by Christensen (1981), since the equations for the species area curves appeared in this study to stabilise quite well by about 40–50 samples, to allow satisfactory extrapolation towards the asymptote. Although there were seasonal differences in species occurrence and number of species recorded on individual samples, the similarity of the cumulative frequency curves for 'winter' and 'summer' (predicting 96 and 90 species/50 samples, respectively) suggests that the method may be robust enough to allow an assessment of species richness without the need to have regard to time of sampling.

The mean number of species recorded from the mammalian dung samples, regardless of dung type, season or region of collection, or the overall species richness of an area, was similar, from nine to twelve. This may suggest that this is an indication of the number of species which can exploit and fruit on any particular sample over the incubation period of 2–3 months. Angel & Wicklow (1983) recorded a similarly consistent, but higher, number of species at any one time in their study of 13 samples of new and old (< 4.5 y) cattle dung and rabbit pellets from three pasture habitats across a mesic to semi-arid environmental gradient in the Great Plains area of north America. They found that although dung of different ages produced similar numbers of species on incubation in moist chambers, the species differed with age. They concluded that the higher diversity of samples from the two semi-arid localities was at least in part due to the long

periods for which dung survived, and that the species assemblage which may be recorded in nature over a relatively long period of exposure to various environmental conditions is not necessarily the same as that which is recorded when relatively new dung is incubated. This is not thought to be a confounding factor in the current study, since a conscious effort was made to obtain relatively recent samples of dung for incubation, but it is a factor which should be borne in mind when considering the completeness of any assessment of the dung mycobiota.

Seasonal occurrence

Wicklow (1981) speculated that an accumulation of inoculum in feeding areas over the growing season might be a reason for greater species richness in winter samples. The tendency to be more frequent in winter samples, observed for some species and the overall species richness of samples in this study, was noted by Bell (1975), in a three-year study of brushtailed opossum dung. She attributed the higher occurrence of some species to greater winter rainfall, but it is possible that temperature could also be a factor, since some species, particularly of *Thelebolus*, are known to be psychrophilic (Bergman & Shanor 1957, Wicklow & Malloch 1971) and rainfall in Britain, from where the majority of records were made, is not particularly or regularly seasonal in occurrence. Bell (1975) never found *Ascozonus woolhopensis* on summer samples. The majority of my records of *A. woolhopensis* were either from samples collected in October to December, or from montane areas, and *Ascozonus monascus*, a new species described from this study (van Brummelen & Richardson 2000) developed on incubation from frozen rabbit pellets collected in December. Bell also found that *Coprinus* spp., *Lasiobolus ciliatus* and *Ascobolus crenulatus* were more frequent in winter, which agrees generally with the current observations, except for *Lasiobolus*, where no trend was found. Examination of latitudinal and seasonal trends (Tables 3–5) shows that for many taxa there is a concordance between those tending to be more frequent in temperate areas (cool and moist) and winter (cool and moist) e.g. *Pilobolus*, *Ascobolus*, *Thelebolus*, *Schizothecium* and *Coprinus*. Those which are more frequent in lower latitudes and summer are *Saccobolus*, *Podospora*, and *Hypocopra*. As might be expected with such a general and observational type of study there are many inconsistencies. The reasons for such seasonal and latitudinal differences may be sought in the relationship between structure and adaptation to various environmental factors. *Podospora* and *Hypocopra*, and other *Xylariaceae*, have coriaceous or stromatic perithecia, which might be more resistant to desiccation than the thinner-walled cells of *Schizothecium* perithecia and apothecia of the *Ascobolaceae* and *Thelebolaceae*. It is, however, difficult to suggest why two such structurally similar genera as *Ascobolus* and *Saccobolus* appear to have different requirements, especially as *Saccobolus* apothecia are generally smaller than those of *Ascobolus*. This feature, while making them more vulnerable to desiccation, might also have conferred on them a ruderal quality – quick to develop and mature. An exception to the temperate nature of *Ascobolus* is *A. immersus*. Its apothecia are relatively large for a coprophilous species of the genus, and with gelatinous matrix in the hymenium, which could confer resistance to desiccation.

Latitudinal gradient

The existence of a gradient of decreasing species richness with increasing distance from the equator is well known and documented (e.g. Rosenzweig 1995, Brown & Lomolino 1998), but there are few reports quantifying such a gradient in the fungi. The main evidence is from tropical rather than temperate mycologists, and is difficult to assess, since it is derived from archival studies and check lists, which by necessity relate to areas of different sizes and habitat complexity, and not to studies which are strictly comparable or, in the case of the tropical component, less complete than the better known temperate mycobiota. Hyde, Wang & Jones (1997) note that there are very few tropical freshwater ascomycetes when compared to those described from temperate areas, but concede that this may be due to lack of sampling. Aptroot & Sipman (1997) compared the lichens in a part of Europe, Papua New Guinea, Colombia and the Guianas, and concluded that there was no great difference in diversity between the tropical and temperate assemblages, but again with the proviso that sources from which the information was obtained for both areas was incomplete. On the other hand, Korf (1997) says 'the impression is that … even in … montane tropical regions species diversity [of discomycetes] far exceeds that known to most temperate collectors … [but] … I have no data to back up such an assertion'. Cannon (1997), in the same volume, does provide convincing evidence of a gradient for the number of species of the *Phyllachoraceae*, where there is a marked decline from the number of species (1064) in a zone 20° either side of the equator, through successive 20° zones (930 and 399) to 66 species in the zones 60–80° N and S of the equator. The gradient observed in the *Phyllachoraceae* is steeper than that found in this study for the coprophilous fungi (approx. 2.7 : 1 for the equatorial : 40–60° zones, compared to approx. 1.5 : 1 for the coprophils). Cannon (1997) notes that the level of habitat diversity is a major factor in species richness per unit area, and figures are affected by the intensity of collecting and differing areas covered. Since species of the *Phyllachoraceae* are foliar biotrophs, often with limited host range, the high diversity of their supporting hosts in the tropics is likely to be correlated with their higher species richness there. The results from this study of coprophils provide, from direct observation, further evidence of a latitudinal gradient of diversity in fungi, increasing towards the equator, both on dung in general and on specific dungs. The observation of a clear gradient on a single substrate is interesting, since it is suggested that increased diversity at lower latitudes is the result of greater habitat diversity, which derives from the relatively larger land area in tropical regions than on any other place on earth (Terborgh 1973, Rosenzweig 1995). With greater herbivore diversity, it might be expected that the mycobiota of the low latitude herbivores would also be more diverse. It is not immediately clear, however, why the mycobiota of a single dung type should also be more diverse as one moves towards the equator. Three contributory mechanisms can be suggested: (1) although the herbivore species is

the same, its diet and local environment is not, which may have an indirect effect on the substrate and its associated fauna and microbiota, and so on its mycobiota; (2) greater speciation on a more diverse assemblage of dung types produces a larger species pool, the less selective of which are able to colonise a new substrate; and (3) wider climatic variation may also allow the development of a larger species pool. Such a feature does, however, suggest that studies of coprophilous fungi could be of use in the detailed analysis of the effect of latitude and other environmental factors in diversity studies, since relatively uniform 'habitats' are available worldwide, in the form of dung from introduced wild and feral domestic mammals (e.g. cattle, horse, sheep, goats, rabbit), thus reducing some of the variables associated with observations from distant and variable habitats.

Substrate composition

The well-known coprophilous succession of phycomycetes ('sugar fungi'), ascomycetes and basidiomycetes has often been explained by ability of these different fungi to use successively more complex substrates. Lodha (1974) suggests, however, that it has less to do with the 'run-down' of nutrients, and can be better explained by the time taken for each fungus to produce its fruiting structures from a simultaneous start to growth when the dung is deposited. This view is, however, complicated by the fact that *Sp. minima*, and so possibly other coprophils, can be isolated from the rumen of sheep and will grow under near-anaerobic conditions (Brewer *et al*. 1972). That *Sp. minima* may already be growing when the dung is deposited would help to explain why it can be found fruiting on relatively fresh dung in the field, but it is also able to continue fruiting for long periods of incubation. Fungi so adapted to grow under such conditions might be expected to appear early in any succession, regardless of the relative proportions of the various nutrients. It is perhaps not surprising that there appear to be no obvious or consistent associations between the relative frequencies of the four main taxonomic groups and the relative chemistry of the different dung types (Table 6) which might simply account for the differences. Subtle differences in substrate composition may explain some of the differences in the mycotas of the different dung types, but such differences are not likely to be found in the absolute or relative amounts of the major components (lignin, cellulose and polysaccharides), which are present in the different dungs at roughly the same general levels, although C/N and L/N ratios vary by factors of *ca* 2–4. There is little information on the detailed composition of dung. Angel & Wicklow (1983) reported 1.5% N in cattle dung < 2 mo old. Raymond (1948), Soni *et al*. (1954), and Lambourne & Reardon (1962) reported N values for sheep dung of 2–5%, in studies of faecal nitrogen levels used as estimators of the quality of feed intake and digestion. The nitrogen levels found in this study are at the lower end of that range. Raymond (1948) found that N levels in sheep dung decreased with increasing herbage maturity, and Brasher & Perkins (1978) reported that N levels in dung of moorland sheep tended to decrease from 2.6% in May to *ca* 2.2–2.3% in September and October. The samples analysed for the present study were from animals which were wild, or grazing at large, in rough pasture, moorland or woodland habitats, so they would not be expected to be consuming high nutrient food, or producing high N dung. This feature is also reflected in the high lignin contents found for grouse, sheep and deer, feeding on moorland, with shrubby *Ericaceae* species, and in woodland. The fact that there are seasonal differences in N content of dung may be a contributory factor to seasonal differences in occurrence of fungi, as well as the temperature factor already suggested. Although no attempt was made to examine the effect of season, year or region on the chemical composition of dung, I do not envisage there being much difference from one year to another and, while there may be differences in different parts of the world, one might expect that a similar metabolism (same animal) and diet would not result in the gross chemistry of the end product being so different as to markedly affect species richness or community composition.

Fungi are unable to use lignin as the sole C source. Ligninases allow access to polysaccharides, e.g. cellulose, which are linked to lignin by hemicellulose (Sinsabaugh & Liptak 1997). The main lignin decomposers are basidiomycetes and members of the *Xylariaceae*, but once the lignin is broken down other fungi have access to the breakdown products (Lodha 1974, Cooke & Whipps 1993). Low N induces ligninase activity, and grouse dung exhibits this feature, with the lowest (but non-significantly different) N level and highest C/N and L/N ratios. At the other end of the range, rabbit and cattle have higher N levels and the lowest C/N and L/N ratios (Table 6). Except for grouse, all C/N levels are below the 30:1 value suggested by Pugh (1974) as the level below which decomposition occurs rapidly. The significantly higher value for grouse dung may partly explain why it supports fewer fungi. Melillo, Aber & Muratore (1982) found that low L/N ratios are more conducive to rapid decomposition of leaf litter of six tree species. Beech litter, with the highest L/N (27) only lost *ca* 5% over a year, while the lowest, ash (L/N = 14) lost about 38%. This range of L/N values is at the higher end of the range found for the six dung types in the current study. Dighton (1997) also noted that C/N and L/N ratios are determinants of the resistance of resources to decomposition, and that cellulose is unavailable when the cellulose/lignin ratio is < 0.5. This value was well exceeded (1.3–4.4) by all of the 6 dung types analysed (Table 6). The low L/N and high cellulose/lignin ratio values for cattle and rabbit in particular indicate that, on this basis, they are better substrates than, for example, grouse droppings.

Given that the dung samples tested contained 50–60% cellulose it is not surprising that many coprophilous fungi can utilise cellulose and hemicelluloses. Wicklow, Detroy & Adams (1980b) identified *Sordaria fimicola*, *A. furfuraceus*, *Pod. decipiens* and *Por. punctata* as early and rapid decomposers of free cellulose, with *Hypocopra merdaria* and a basidiomycete appearing later as cellulose decomposers. *Poronia oedipus* (Denison & Koehn 1977), species of *Ascobolus*, *Podospora* and *Sordaria* (Taj-Aldeen, Al-Habbeb & Abdullah 1990), *Iodophanus* and *Thecotheus* (Pardo, Sivori & Ranalli 1997) and *Saccobolus saccoboloides* (Magnelli & Forchiassin 1999), are reported to be cellulolytic or to produce cellulases. These

studies also indicate, however, that generalisations at the generic level cannot be made, since *Podospora similis* was an effective cellulase producer, while *P. decipiens* (and *Lasiobolus ciliatus* and *Sp. minima*) was not (Taj-Aldeen *et al*. 1990). The genera with cellulolytic species in this paragraph provide the majority of records in this study, and it does not seem as if relatively small differences between the amounts of cellulose or other complex carbon compounds can be used to explain the different community composition of the different mycobiotas. The grouse, hare and rabbit dungs had similarly high amounts of cellulose, and the grouse and hare had very similar high levels of lignin, but their species richness and community composition were very different. Given that the grouse droppings are the result of a completely different metabolism from that of the mammalian herbivores, it is perhaps not surprising that their mycobiota is different. Although they had the highest level of soluble carbohydrate and starch (5.1%), there was a complete absence of the typical coprophilous zygomycetes (e.g. *Pilaira*, *Pilobolus*, *Phycomyces*) which may be due to the nature of the nitrogen compounds in bird dung, including uric acid, which most fungi are unable to metabolise. It is also a puzzle to find that *Sp. minima* is the dominant species on grouse pellets, in view of reports that few fungi apart from basidiomycetes can utilise lignin, that ligninases facilitate the breakdown of lignin into the more accessible cellulose and hemicelluloses, and that *Sp. minima* cannot degrade free cellulose (Taj-Aldeen *et al*. 1990). There are very few reports of coprophilous fungi using lignin. Wicklow *et al*. (1980b) found that an unidentified basidiomycete caused significant loss of lignin, but a *Coprinus* sp. did not. The majority of coprophilous basidiomycetes are *Coprinus* spp., so the organisms responsible for the breakdown and utilisation of the 13–38% lignin of which herbivore dung is comprised have still to be identified.

Cooke & Rayner (1984) note that the collective physiological attributes of coprophilic fungi closely resemble those found in litter decomposing communities. This might be expected, since the composition, if not structure, of herbivore faecal material will be similar, but differences in the specific composition of the mycobiota can be explained by the fact that the 'litter' has been subjected to anaerobic conditions and higher than ambient temperatures in the gut. Further, the litter substrate exists as an essentially permanent habitat, while the dung habitat exists as a series of relatively short-lived 'islands'. Consequently, the coprophilous mycobiota has adapted to accommodate these factors, by developing strategies to survive passage through the gut, and elegant and effective spore dispersal mechanisms, both active and passive. Wicklow, Angel & Lussenhop (1980a) fed rabbit and sheep with the same alfalfa hay, and found that the relative abundance pattern of species occurrence on the two dungs did not differ, but that there were more apothecial species on the sheep dung and more perithecial fungi on rabbit. They concluded that the 'herbivore digestive process is of fundamental importance in determining species composition and structure of the coprophilous mycota, and environmental factors will determine how the community expresses itself'. This is borne out by the differences observed in the current study, particularly in relation to the differences observed between the coprophilous mycobiotas of the two lagomorphs, the ruminants and the grouse.

Rare species

What constitutes rarity? Many species of specialised habitats may be widespread but demonstrate what might be called apparent or pseudorarity simply because of lack of observation. For readily observed fungi a lack of records is an indication of true rarity, but for those which are not the rarity may be an artefact. Some case studies illustrate the phenomenon.

(1) *Ascobolus carletonii*, described by Boudier (1913) from capercaillie dung from Scotland, was subsequently recorded in Yorkshire (Mason & Grainger 1937; no details of this record are known), from grouse dung in Scotland in 1966 and 1967 (Richardson 1972) and from capybara dung from near Rio de Janeiro, Brazil, in 1989 (van Brummelen 1990). No other records are known predating the current study; only five collections in 80 years. Without informed knowledge such species might be considered rare or even endangered. In the current study it was the second most frequent species on grouse dung, and was recorded from 41% of the 29 samples examined, and not from any other substrate. It is clearly one of Lundqvist's fastidious species, even allowing for the unusual occurrence on capybara dung in a completely different part of the world. If the appropriate substrate is collected and incubated it should be readily observed if present.

(2) Observational difficulty is another reason for pseudorarity. The two coprophilous *Phomatospora* spp. have very small perithecia, which are almost totally immersed apart from a tiny erumpent ostiole, and they develop late in the incubation period. Even when one knows what to look for they are inconspicuous. *P. coprophila* is widespread in Britain, especially on sheep (present on 32% of samples) and deer and cattle (13%) dung. I have not found *P. minutissima* in Britain, but have records from France (cattle), Australia (wallaby, grey kangaroo and cattle) and Brazil (cattle, deer and sheep), and Lundqvist (1981) notes that it is not uncommon, especially on cattle, in the southern part of Sweden.

(3) Apparent scarcity may also result from the fact that incubation conditions which favour most fungi are unsuitable for some. Webster *et al*. (1999) and Webster & Weber (2000) have observed that stromata of some species of *Xylariaceae* will only produce mature perithecia and spores, which are necessary for identification, if they are incubated for long periods at very low rh (*Wawelia* spp.) or buried in soil (*Podosordaria tulasnei*). A reluctance to record even a common fungus, because it cannot be identified with certainty, will give the impression that it is rare, although hindsight coupled with notes from earlier observations can sometimes be used to modify the record.

(4) Searching effort is also important. Richardson (1970) showed that very frequent recording is needed to achieve complete observation of agaric fruiting bodies in a woodland habitat. Weekly recording would result in 10–30% of fruit bodies not being observed, increasing to 40–60% for two-weekly recording. The analogy applies also to the microfungi. Scans of pellets do not allow reliable identification of many species to be made without removal and examination at

Table 7. Comparison of occurrence (%) of common ascomycetes on dung of domesticated and wild mammals over two periods.

	Domestic (cattle, sheep)		Wild (rabbit, hare, deer)	
	n = 56 1964–1969	n = 74 1994–1999	n = 77 1964–1969	n = 186 1994–1999
Sporormiella intermedia	57	35 (46)*	54	48 (67)
Schizothecium vesticola	61	70 (74)	49	44 (78)
Lasiobolus cuniculi	57	24 (24)	34	18 (21)
Thelebolus nanus	48	43	36	27
Ascobolus albidus	39	34	43	31
Schizothecium conicum	46	70	26	21
Ascobolus immersus	55	59	16	10
Podospora decipiens	34	58	21	27
Saccobolus versicolor	30	38	20	47
Iodophanus carneus	36	53	11	23
Viennotidia fimicola	14	18	31	30
Ascobolus stictoideus	20	20	18	6
Thelebolus microsporus	25	26	13	4
Ascobolus furfuraceus	20	12	16	4
Coniochaeta scatigena	23	15	10	25
Ryparobius polysporus	14	1	16	16
Phomatospora coprophila	29	30	3	3
Thelebolus stercoreus	4	1	26	16
Podospora appendiculata	7	3	18	13

* Values in brackets include records of *Sp. australis*, *Sch. tetrasporum* and *Lasiobolus* spp. (see text).

higher magnification. At each inspection one removes what seems to be a representative collection of the different species present, but there is always the possibility that an infrequent species will not be observed. Repeated, frequent and thorough inspection of samples until no further new species are found will help to reduce the possibility of infrequent species being missed. In the case of coprophils on incubated dung this period can extend to several months.

Monitoring and assessment

Hyde & Hawksworth (1997) have addressed the difficulties involved in measuring and monitoring biodiversity. They consider that even RBA (rapid biodiversity assessment) and RTU (recognisable taxonomic unit) techniques are generally not feasible for microfungi, since their diversity is so great that it would not be practical to train paratechnicians to an effective level within the time scales available. The use of RTUs would provide little taxonomic information, and there is need to do more than count. They consider that there are insufficient data on which to base a decision on the most representative microhabitat to select as indicator of mycological species richness and, if RBA or RTU methods are to be used, there is first a need for specific research to provide data to identify indicator habitats. Coprophils could, however, be useful as indicators of biodiversity or habitat quality, and two examples are given.

The existence of species lists from extensive studies of a particular habitat allow them to be used to monitor the effects of change. A comparison of the results from the British samples in this study with those of a smaller survey of British samples in 1964–69 (Richardson 1972) shows that there are many similarities in both the list of common fungi and their relative abundance (Table 7). Data from horse and grouse were omitted from the earlier and current data sets, respectively, to ensure that the comparison was based on a similar collection of substrates. The data were also divided into subsets from domesticated (sheep and cattle) and wild (rabbit, hare and deer) animals to increase any possibility of detecting any effect of veterinary treatments which might have changed over the intervening 30 years. Although most of the animals from which samples were collected were wild, or grazing at large, changing patterns in, e.g. the routine use of antibiotics in animal husbandry, and the use of fungicides and insecticides on crops, including pasture, may well have direct or indirect effects on the ecology of coprophilous organisms. Antihelminthics, based on avermectins produced by *Streptomyces avermectilis*, are widely used to control gastrointestinal parasites of cattle. These can affect the insect fauna of dung (Skidmore 1999), which in turn affects its texture and consistency, which is an important factor influencing the mycobiota (Dickinson & Underhay 1977). A reassessment of the taxonomic status and identification of some of the earlier records means that the results for some species are not strictly comparable. Records in Richardson (1972) of *Sch. vesticola* will include *Sch. tetrasporum*, and *Sp. intermedia* will include *Sp. australis*, and most *Lasiobolus* spp. were recorded as *L. ciliatus*. These taxonomic discrepancies are not thought to have any great bearing on the general conclusion to be drawn overall, which is that there has been little change in the composition of the coprophilous mycobiota of common domestic and wild herbivores in Britain over a 30 yr period. This cannot, of course, be linked directly to any changes or otherwise in the farming or natural environment, since no details of the use of such products or environmental changes in the areas in Britain in which collections were made are presented.

The second example is from a subsequent set of thirteen samples collected in June 2000 from the Souss Valley area of southern Morocco. They were collected from areas badly

degraded by grazing sheep and goats, with little vegetation. These were either dry river beds or low density argan (*Argania spinosa*) forest on dry stony soil, with the understorey replaced by cultivation of wheat and barley which had been harvested and cultivated at the time of sampling. Subjectively, the area did not appear to be biologically diverse, and the climate was severe, with extremely high daytime temperatures (30–40 °C) and little or no rain for long periods. These samples, after incubation in the same way as the samples for the main study, yielded 47 species, and a cumulative frequency curve forecast of 80 species per 50 samples. From the worldwide results of the main study a value of *ca* 146 would be expected for a latitude of 30°N (Fig. 6). Although based on a smaller number of samples than the minimum suggested earlier of 40–50, the Moroccan data support a hypothesis that the diversity of samples from a habitat subjectively identified as degraded may be lower than that of samples from areas which supported natural or cultivated vegetation – pasture, grassland, woodland or mountain vegetation – which were the origin of the majority of samples in the worldwide study. The investment required to obtain a quantitative estimate of the species richness of the coprophilous fungi in the degraded Moroccan habitat was relatively small. The samples were incubated for up to 10 wk, until no new records had been observed for some time, with 8–15 examinations, and total examination time for the set of thirteen samples was approx. 40 h. Lawton *et al*. (1998), in assessing the impact of forest modification in one tropical locality, concluded that 'a detailed inventory, even from one area ... will require huge scientific effort', and their work, inventorying eight animal groups along a disturbance gradient in Cameroon, required a total of 10000 h (50 h for 78 bird species to 6000 h for 374 nematode species, 90% of which were unnamed). Clearly, surveying coprophilous fungi would not be appropriate for such a study, partly for reasons of scale, but in some circumstances they may be of use in allowing quick, simple and inexpensive quantitative assessments to be made.

These two particular examples, and the general principles of ecological and community structure demonstrated in this study, show that a simple observational and inexpensive survey of a particular and specialised microcosm can provide information relevant to larger scale ecosystems.

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Corresponding Editor: S. Isaac