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Food preferences of earthworms for soil fungi

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Summary

Soil fungi are considered to be an important food source for earthworms. Selection experiments were carried out in order to study the preferences of earthworm species for a variety of soil fungi. Nine fungal species (*Cladosporium cladosporioides*, *Rhizoctonia solani*, *Mucor* sp., *Trichoderma viride*, *Fusarium nivale*, *Phlebia radiata*, *Glaeophyllum trabeum*, *Coniophora puteana*, *Coriolus versicolor*) were grown separately in centrifuge tubes on sterilized sand with potato dextrose. Tubes containing different fungal species, 8-9 per experiment, were arranged in a food choice arena. The preference for the fungi of 5 different earthworm species (*Lumbricus terrestris*, *Lumbricus castaneus*, *Aporrectodea caliginosa*, *Aporrectodea rosea*, *Octolasion cyaneum*) was tested by adding one specimen per chamber. Removal of sand from the tubes within 6 days was used as the indicator of preference by earthworms. The food preference of earthworms irrespective of ecological group followed a general pattern. *F. nivale* and *C. cladosporioides* were the preferred fungal species, followed by fast-growing species such as *Mucor* sp. and *R. solani*. In contrast, basidiomycetes were generally refused. The epigeic species *L. rubellus* had the strongest preference for a single fungal species, in contrast the endogeic species *A. rosea* fed more evenly on different fungal species. We conclude that early successional fungal species are used as cues by earthworms to detect fresh organic resources in soil.

Key words: Earthworms, soil fungi, food selection

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Introduction

Earthworms use a wide variety of organic materials as food. However, food resources of earthworms belonging to different ecological groups (sensu Bouché 1977) differ considerably. Epigeic (e.g. *Lumbricus rubellus*) and anecic species (e.g. *Lumbricus terrestris*) feed mainly on surface litter, whereas endogeic species (e.g. *Aporrectodea caliginosa*, *Aporrectodea rosea*, *Octolasion cyaneum*) consume large quantities of soil and associated organic residues.

Food preference experiments have shown that earthworms do not feed at random. Significant differences in litter selection are well documented, showing a general preference for leaves with high N content and low levels of plant secondary metabolites (Edwards & Lofty 1977; Lee 1985; Hendriksen 1990). However, in the natural environment plant residues are quickly colonized by microorganisms; senescing leaves are commonly inhabited by bacteria and their protozoan grazers (Bamforth 1973), and can even be invaded by saprotrophic fungi before they reach the soil surface (Deacon 1997). Leaf litter with high contents of secondary metabolites, such as beech, can only be consumed by earthworms after a whole year of seasoning and 'microbial conditioning' (Schaefer 1991). Therefore, microorganisms are an unavoidable constituent of earthworms' food resources, and in particular protozoa and fungi are assumed to form a substantial part of their diet (Edwards & Fletcher 1988; Brown 1995; Bonkowski & Schaefer 1997).

In contrast to bacteria and actinomycetes, which have been shown to be little preferred (Cooke & Luxton 1980) and failed to enable earthworm survival in pure culture, earthworms gained weight when reared in cultures of certain fungal species (Edwards & Fletcher 1988). Examinations of gut contents and casts have shown that large numbers of soil fungi are present in the intestines of earthworms and at least partially digested during gut passage (Domsch & Banse 1972; Dash et al. 1986; Wolter & Scheu 1999). In addition, high numbers of fungal propagules in casts compared to surrounding soil suggest that selective feeding on fungi may occur (Tiwari & Mishra 1993). Hence, soil fungi have been considered to be a major food source for earthworms (Piearce 1978; Edwards & Fletcher 1988; Brown 1995; but see Wolter & Scheu 1999).

Food preferences for certain fungal species by earthworms may play an important role in affecting fungal communities in soil. It has been shown that earthworms are able to reduce the disease severity caused by *Rhizoctonia solani*, the causative agent of 'Rhizoctonia bare patch' disease (Stephens et al. 1993; Stephens & Davoren 1997) and disease caused by the take-all fungus *Gaeumannomyces graminis* (Stephens et al. 1994a). However, the effects depend on earthworm species (Stephens et al. 1994b) and the mechanisms are little understood (Stephens et al. 1993, 1994c).

We carried out feeding choice experiments with five earthworms species in order to compare their preferences for different soil fungal species. Since we expected feeding preferences to differ between species ingesting mainly litter material or soil, we compared the preferences of earthworm species belonging to different ecological groups.

Materials and Methods

Nine soil fungal species taken from the collection of fungi at the Scottish Crop Research Institute, (*Cladosporium cladosporioides*, *Rhizoctonia solani*, *Mucor* sp., *Trichoderma viride*, *Fusarium nivale*, *Phlebia radiata*, *Glaeophyllum trabeum*, *Coniophora puteana*, *Coriolus versicolor*) were grown separately in centrifuge tubes on sterilized sand with potato dextrose. Tubes containing different fungal species, 8–9 per experiment, were arranged in a food choice arena. The food choice chambers consisted of aluminium plates with equally spaced centrifuge tubes penetrating the rim of the plates at the bottom (cf. Doube et al. 1997). Each plate contained three layers of moist filter paper to prevent earthworms from desiccation and was closed with a cardboard lid. Food preferences of five different earthworm species belonging to three ecological groups (the anecic species *L. terrestris*, the epigeic species *L. rubellus*, and the endogeic species *A. caliginosa*, *A. rosea* and *O. cyaneum*) were tested by adding one specimen to each of six replicate chambers. Removal of sand containing the fungal species within 6 days was used as indicator of food preference of the earthworms. For comparing removal rates among earthworm species, the consumption of sand per unit earthworm body weight was calculated. Differences in consumption rates were log-transformed and analysed by a one factorial ANOVA and subsequent Tukey tests for separating differences among means.

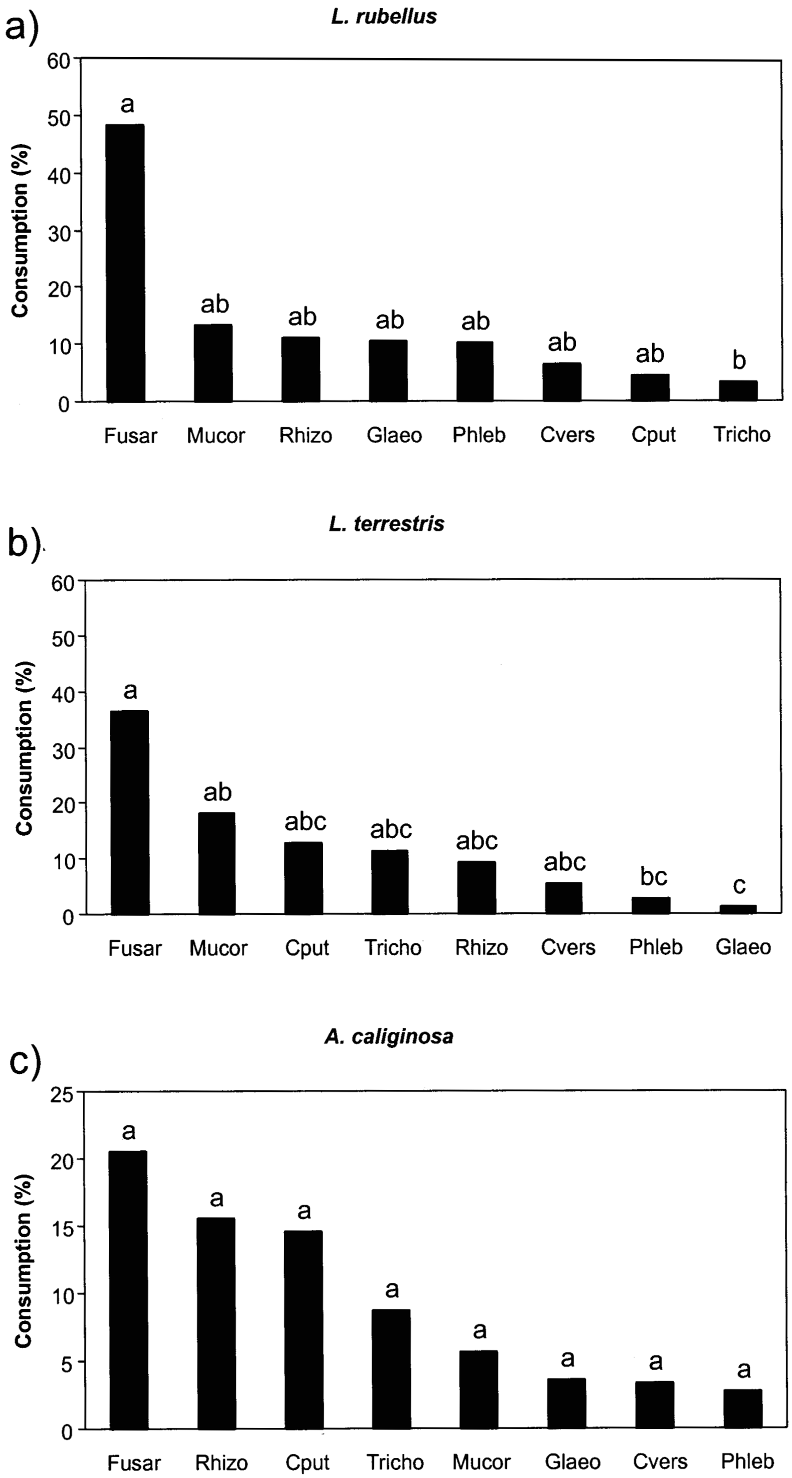
Results and Discussion

When feeding on organic matter, earthworms are ingesting a whole range of food materials, including bacteria, fungi, algae, protozoa and nematodes (Brown 1995). Our food-choice tests demonstrated that earthworms belonging to different ecological groups differentiate between saprotrophic fungi and select certain fungal species (Table 1).

The different earthworm species in our experiment had very similar preferences (Fig. 1a–e). The plant pathogens *F. nivale* and *R. solani* were among the most preferred fungal species. *Mucor* sp., a fast growing pioneer saprotrophic fungus, was also preferred by most earthworm species. In contrast, the basidiomycetes *C. puteana*, *P. radiata*, *G. trabeum* and *C. versicolor* were generally poorly consumed (Fig. 1a–e). In accordance with our results, Moody et al. (1995) found corresponding feeding preferences of *L. terrestris* and also for the anecic species *A. longa* and the endogeic *Allolobophora chlorotica*. In their experiments Fusarium sp. was most preferred, while *Mucor* sp. and *Trichoderma* were consumed slightly less frequently and *Chaetomium* sp. and the basidiomycetes *Sphaerobolus* sp. and *Agrocybe* sp. were significantly less often taken (Moody et al. 1995).

Table 1. Results of multiple choice feeding tests with 8 or 9* different fungal species by the earthworms *Lumbricus rubellus*, *Lumbricus terrestris*, *Octolasion cyaneum*, *Aporrectodea caliginosa* and *Aporrectodea rosea*. F-values, P-values and sum of squares explained (% SS) of a one factorial ANOVA

	L. rubellus	*L. terrestris*	*O. cyaneum**	*A. caliginosa*	*A. rosea**
F-value	8.7	4.0	2.4	2.5	2.1
P-value	0.0001	0.002	0.03	0.03	0.067
% SS explained	60.4	41.1	30.0	30.4	31.3


a)
L. rubellus
Consumption (%)
0
10
20
30
40
50
60
a
ab
ab
ab
ab
ab
ab
b
Fusar
Mucor
Rhizo
Glaeo
Phleb
Cvers
Cput
Tricho
b)
L. terrestris
Consumption (%)
0
10
20
30
40
50
60
a
ab
abc
abc
abc
abc
bc
c
Fusar
Mucor
Cput
Tricho
Rhizo
Cvers
Phleb
Glaeo
c)
A. caliginosa
Consumption (%)
0
5
10
15
20
25
a
a
a
a
a
a
a
a
Fusar
Rhizo
Cput
Tricho
Mucor
Glaeo
Cvers
Phleb

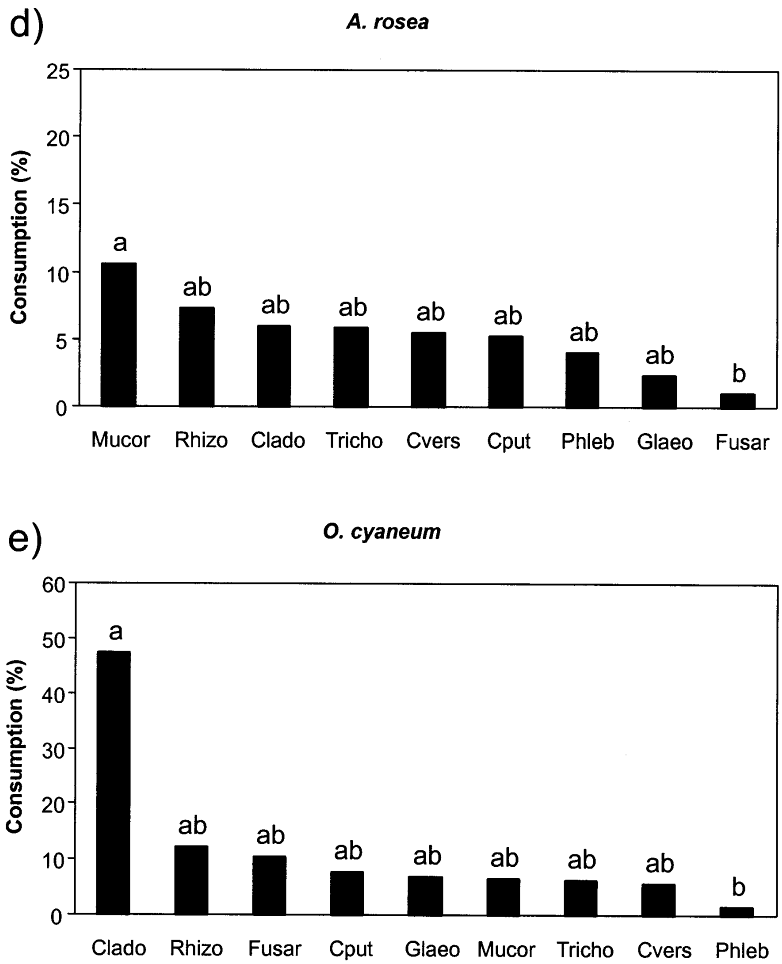


Fig. 1. Consumption (% consumption g^{-1} body fresh wt) of different fungal species (Clado: *Cladosporium cladosporioides*; Rhizo: *Rhizoctonia solani*; Mucor: *Mucor* sp., Tricho: *Trichoderma viride*; Fusar: *Fusarium nivale*; Phleb: *Phlebia radiata*; Glaeo: *Glaeophyllum trabaeum*; Cput: *Coniophora puteana*; Cvers: *Coriolus versicolor*) by the earthworm species *Lumbricus rubellus*, *Lumbricus terrestris*, *Aporrectodea caliginosa*, *Aporrectodea rosea* and *Octolasion cyaneum*.
Backtransformed means of log-transformed data. Bars with different letters are significantly different (Tukey-test, $P < 0.05$)

Due to a contamination of our *Cladosporium* cultures during the experiment, only food choice experiments with the endogeic earthworm species *A. rosea* and *O. cyaneum* contained the dark-pigmented fungus *Cladosporium* sp. *O. cyaneum* showed a particularly strong preference for this fungus. *Cladosporium* was among the three fungal species most preferred by *A. rosea*, even though this earthworm species generally had low preferences (Table 1).

Other food-selection experiments add evidence to the assumption that dark pigmented Dematiaceae, particularly *Cladosporium*, are generally a preferred food source of lumbricid earthworms. Feeding experiments testing earthworm survival on 16 different soil fungal species showed that the compost worm *Eisenia foetida* grew well only on two species, *Cladosporium* sp. and *Arthrobothrys* sp., and less on *Aspergillus* spp., *Ascobolus* sp. and *Trichoderma* sp. and the earthworms died within 6 weeks when feeding on other fungal species, including *Fusarium* sp., *Penicillium* sp., *Aspergillus* spp. and *Oidium* sp. (Edwards & Fletcher 1988). Also Marfenina & Ishchenko (1997) stated from their food choice experiments that dark melanin-containing fungi, such as *C. cladosporioides* are most attractive for *E. foetida*. Cooke (1983) included two members of the Dematiaceae *Alternaria* and *Cladosporium* in preference tests with *L. terrestris*. Although the earthworms were less selective for *Cladosporium*, they preferred the dark pigmented *Alternaria* together with *Fusarium* sp. and *Trichoderma* sp., while filter paper discs inoculated with *Poronia* sp., *Chaetomion* sp. and *Penicillium* sp. were poorly consumed (Cooke 1983). Similarly, by extracting soil fauna from fungal baits, Dash & Cragg (1972) showed that fungal preferences of enchytraeids generally matched preferences of other soil organisms, including insect larvae, Collembola, Acari and nematodes, and confirmed a particularly strong preference for *Cladosporium*. In addition, Dematiaceae like *Cladosporium* are assumed to be commonly preferred over hyaline fungi by Collembola and mites (Klironomos et al. 1992; Kaneko et al. 1995; Klironomos & Kendrick 1996; Maraun et al. 1998), indicating that Dematiaceae are generally of high food quality for soil animals.

Basidiomycetes, which are characteristically degraders of recalcitrant polymers, seem to be of low food quality. The basidiomycetes in our study included brown and pocket-rot types (*P. radiata*, *G. trabeum*) and the white-rot *C. versicolor*, and were generally refused. This finding corresponds well with the rejection of cellulose (*Chaetomium*) and cellulose and lignin degraders (*Sphaerobolus*, *Agrocybe*) by *L. terrestris*, *A. longa* and *A. chlorotica* in the study of Moody et al. (1995). However, preferences for the dry-rot fungus *C. puteana* in our study were in the same range as those for *Trichoderma*, indicating that some basidiomycetes may overlap in the sequence of preferences with some less preferred non-basidiomycete fungi.

Trichoderma was generally consumed less often by earthworms than *Fusarium*, *Mucor*, *Rhizoctonia* or *Cladosporium* in our study, but more often than basidiomycetes, indicating an intermediate position in preference in comparison to the other fungal species offered. *E. foetida* has been shown to survive on *Trichoderma* (Edwards & Fletcher 1988; Hand & Hayes 1988), but the extensive feeding study by Morgan (documented in Edwards & Fletcher 1988) which included 18 bacterial and 16 fungal species indicated that *Trichoderma* is only of intermediate food quality for *E. foetida*.

Earthworm preferences for fungal species are strikingly similar to preferences reported for enchytraeids (Dash & Cragg 1972) and soil microarthropods. Collembola preferred *Fusarium oxysporum*, over *Rhizoctonia* sp. and *Phytium* sp. but rejected

Trichoderma, *Penicillium* and *Aspergillus* (Wiggins & Curl 1979). In other studies, Collembola preferred *R. solani* over the three biological control fungi *Trichoderma*, *Laetisaria* and *Gliocladium* (Curl 1979; Curl et al. 1988), and over *Trichoderma*, *Penicillium* and *Aspergillus* (Wiggins & Curl 1979), and the ectomycorrhizal basidiomycetes *Hebeloma*, *Paxillus* and *Rhizopogon* (Hiol Hiol et al. 1994). Feeding experiments by Chen et al. (1995) also showed a general agreement in food preferences of four collembolan species for Mucorales (*Mucor* sp., *Absidia* sp.) over *Penicillium* sp. and *Humicola* sp.

From published data and our present experiment it appears that dark-pigmented fungi (Dematiaceae; e.g. *Cladosporium*, *Alternaria*) together with plant pathogens like *Fusarium* and *Rhizoctonia* seem to be most preferred. *Mucor*, a pioneer saprotrophic genus is also among the more preferred fungi, but according to Moody et al. (1995) ranked below that of *Fusarium*. *Trichoderma* was often consumed, but was not among the more preferred fungi (Edwards & Fletcher 1988; Hand & Hayes 1988; this study). We did not include *Penicillium* species in our study, but evidence from other studies suggests that they are not preferred by earthworms (Cooke 1983), enchytraeids (Dash & Cragg 1972), Collembola (Wiggins & Curl 1979; Chen et al. 1995) and oribatid mites (Maraun 1997; Maraun et al. 1998).

Food preferences and fungal succession

The observed general similarities among different earthworm species, enchytraeids and soil arthropods suggest a general underlying mechanism which shapes soil faunal feeding preferences.

Animals in soil, including earthworms, are generally confronted with the difficulty of living in an opaque environment where they are surrounded by a nutritionally poor mixture of mineral particles and organic matter. High amounts of detritus in gut contents of endogeic earthworms compared to the surrounding soil indicate selective feeding rather than indiscriminate ingestion of soil material (Judas 1992). The detection of nutrient-rich hotspots in soil is difficult and therefore can be assumed as a strong evolutionary force and a crucial prerequisite for earthworm survival.

Possible explanations for fungal preferences by earthworms focus on the nutritional value of the fungus, or the presence of antibiotics or other deterrent metabolites in or around the mycelia. Even though the experiments demonstrate distinct preferences between soil fungi by earthworms, in the natural environment the animals cannot be expected to graze specifically on certain fungal species since earthworms co-consume large quantities of soil and organic matter. In the soil, food selection of earthworms is inevitably confounded by the fact that fungi colonize decomposing plant remains and earthworms ingest those remains, together with the associated microbial flora and microfauna.

Studies on fungal successions have shown that *Cladosporium* and *Phoma* are primary colonizers on decomposing oak leaves followed by *Alternaria*, *Trichoderma* and *Aspergillus*, while *Penicillium* colonized the leaves only after four months (Singh et al. 1990). Similarly, Howard & Robinson (1995) demonstrated that decomposing wheat straw particles during early succession were preferentially colonized by *Fusarium*, *Cladosporium* and *Mucor*, i.e. the most preferred fungal species by earthworms, while other species, like *Penicillium* and *Trichoderma* occurred at random and generally colonized the plant residues during the later stages of succession. We assume that this coincidence holds a significant key for understanding earthworm preferences for soil fungi. Fungi characteristic of early successional stages of decomposition are indicators of a relatively new and nutrient rich organic resource. The ability of earthworms to discriminate between fungal species of different successional stages may be a mechanism by which relatively new and nutrient rich organic resources in the opaque soil environment can be located. Therefore, considering the ecological role of fungi as members of communities of decomposing plant residues may provide a deeper insight in the underlying mechanisms than simply referring to food preferences of earthworms.

The observed food preferences of earthworms provide evidence for this hypothesis. The most preferred fungi by earthworms include many pathogens or parasites of plant tissue which commonly attack either juvenile plants (*Rhizoctonia*) or plants beginning to senesce (*Cladosporium*, *Fusarium*). These fungi remain active for some time after plant remains enter the soil, usually by exploiting the more readily utilizable resources, and thus enter the decomposer sequence (Deacon 1997). As soon as plant residues reach the soil surface, zymogeneous fungi with a short exploitative growth phase, like the common *Mucor* spp. enter the decomposer chain as pioneer saprotrophs. They are weak competitors and do not produce antibiotics but are intolerant of antibiotics of other fungi. Consequently, the pioneer saprotrophic fungi are soon replaced by polymer degrading fungi (e.g. *Trichoderma*, *Penicillium*), i.e. by species utilizing more recalcitrant compounds. Once established, these fungi tend to defend the resources against potential invaders, either by sequestering a critical limiting nutrient (e.g. nitrogen) or by producing inhibitory metabolites (Deacon 1997). The food quality of plant residues is drastically reduced once polymer degraders have entered the sequence of decomposer fungi, making both fungi and organic matter less attractive for earthworm consumption. Thus plant residues in soil colonized by plant pathogens and pioneer saprotrophs indicate fresh and nutrient rich resources in addition to fungal mycelia for saprotrophic animals like earthworms, while plant remains colonized by polymer degrading fungi and basidiomycetes represent an already highly exploited and unattractive (secondary metabolite based) food resource. Thus earthworms and fungi can be assumed to compete in the exploitation of fresh organic matter.

Similarly, Scheu & Schaefer (1998) postulated a severe competition between microorganisms and earthworms for available nutrients, since earthworms and microorganisms responded conversely to the manipulation of food resources by addition of carbon and nutrients in a field experiment. Microbial biomass has been shown to decrease only insignificantly after gut passage of earthworms (Scheu 1987; Wolter & Scheu 1999; Tiunov & Scheu 2000), adding further evidence that earthworms are not primarily dependent on microorganisms as a food source.

The selectivity for fungal species differed considerably among earthworm species in our experiment (Table 1), indicating differential use of fungi as food or food indicators by earthworms. The detritivore species *L. rubellus* and *L. terrestris* strongly preferred certain fungi and removed 48 and 36 % of their most preferred species, respectively, whereas the geophagous species *A. caliginosa* was less selective removing only 21 % of its most preferred species. Preferences of *O. cyaneum* and *A. rosea* are not directly comparable, since the number of fungi in the experiment was expanded by *Cladosporium* sp., but particularly the endogeic *A. rosea* showed the least selectivity consuming only 11 % of its most preferred species (Fig. 1d).

Detritivore epigeic and anecic earthworm species are important consumers of litter material which is generally densely colonised by fungi. These species have been shown to be more selective in their food choices (Hendriksen 1990) and the distinctive preferences for certain fungal species by the epigeic *L. rubellus* and anecic *L. terrestris* are in accordance with our expectations. In contrast, the geophagous endogeic species *A. caliginosa* and particularly *A. rosea* were less selective and consumed less material. Endogeic species consume high amounts of mineral soil (Judas 1992) and rely less on fresh litter resources. These findings have important implications for the biocontrol potential of earthworms. Investigations by Stephens et al. (1994 b, 1997) indicated that *A. rosea* was less effective in reducing *R. solani* disease severity on different plants than *A. trapezoides*. The natural abundances of stable isotopes in earthworms clearly demonstrated a different trophic position of *A. rosea* in comparison to coexisting endogeic *A. caliginosa* and *A. chlorotica* in the field (Schmidt et al. 1997). This is in accordance with our results, since *A. rosea* was the least selective of all tested earthworm species.

In conclusion, we suggest that earthworms and fungi are competing for the same food resource i.e. organic matter in an early stage of decomposition. Even though fungi of early successional stages are preferred and partly digested, fungi are considered to function primarily as indicators of food quality to earthworms and other microbi/detritivores in soil.

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