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Sympatric coevolution of the trophic niche of two detritivorous isopods, Asellus aquaticus and Proasellus coxalis

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The role of 16 species of microfungi in the potential trophic niche of populations of *Asellus aquaticus* (L.) and *Proasellus coxalis* Dolff. collected in both sympatry and allopatry was determined in the laboratory. Animals and fungi were collected in three woodland streams similar as to geographic location and hydrogeologic, physical and chemical features. The fungi were offered as the sole food source to the animals for 50 d. Young animals, born in the laboratory, were tested for their trophic potential. Sympatric *A. aquaticus* and *P. coxalis* had a much more differentiated potential trophic niche than allopatric populations. In particular, the sympatric species had a potential overlap in the use of 25% of the tested fungi, while allopatric species had a potential overlap of 75% of the fungi. The two species from sympatric locations were specialized on fungal species not very common in nature, while more common fungi were used without distinction by both species. The exclusiveness of each fungal species for the isopods living in sympatry increased inversely to its frequency in nature. The results suggest a possible effect of co-occurrence on the character displacement shown by sympatric populations and support the hypothesis of coevolutionary trophic partitioning between them. The results also imply that the importance of the fungi in the co-occurrence of the isopod species is greater than suggested by the small biomass of the fungi.

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Исследовали роль 16 видов микроскопических грибов как потенциальной трофической ниши у симпатрических и аллопатрических популяций *Asellus aquaticus* (L.) и *Proasellus coxalis* Dolff. в лабораторных условиях. Животные и грибы были собраны в трех лесных речках, сходных по географическому положению, гидрологическому режиму, физическим и химическим особенностям. Грибы предлагали животным для еды в течение 50 дней. У молодых животных, родившихся в лаборатории, исследовали потенциальную пищевую избирательность. У симпатрических *A. aquaticus* и *P. coxalis* потенциальные трофические ниши различаются гораздо сильнее, чем у аллопатрических популяций. В частности, симпатрические виды показали потенциальное перекрывание в потреблении 25% исследованных видов грибов, а аллопатрические виды – потенциальное перекрывание 75% видов грибов. Два вида из симпатрических местообитаний специализированы на видах грибов, не очень часто встречающихся в природных условиях, а более обычные грибы использовались без выбора обоими видами мокриц. Исключение из диеты каждого вида грибов у изопод, живущих в симпатрических условиях, возрастает в обратной зависимости от их частоты в природных условиях. Результаты показали возможность влияния совместной встречаемости на характер сдвига, наблюдаемый у симпатрических популяций и подтверждает гипотезу о коэволюционном разделении трофических связей между ними. Результаты также показали, что значение грибов в совместной встречаемости отдельных видов изопод больше, чем это диктуется малой биомассой грибов.

Introduction

The hypothesis that competition is an important factor in coevolutionary processes is widely shared (MacArthur 1970, Connell 1980). In spite of all the theoretical attention given to this subject, it is uncommon to find direct proof of coevolution in present-day species. We can observe allopatric and sympatric populations assuming that the former condition precedes the latter in time. If the areas studied are basically similar we may suggest that possible differences between conspecific populations are a response to competition rather than an adaptation to the environment. This method of studying coevolutionary processes is perhaps the best of non-experimental methods, especially in benthic communities of lotic environments (Connell 1980).

On the other hand, very little is known about coevolutionary trophic partitioning between benthic detritivorous animals. The importance of microfungi present on plant detritus in the diet of these animal groups has been ascertained: detritivorous animals select detritus according to the type of microfungal colonization (Bärlocher and Kendrick 1973, Cummins and Klug 1979, Rossi et al. 1981). Moreover, in populations of two species of isopods co-occurring in a biotope in Southern Italy, we showed a strong trophic dependency of the animals on the fungi and noted a high interspecific differentiation in the capacity of exploiting the various fungus strains offered as food (Rossi and Fano 1979). Our data did not permit speculation as to the evolutionary nature of the phenomenon, so in the present study attention was given to potential trophic niches of allopatric and sympatric populations of *Asellus aquaticus* (L.) and *Proasellus coxalis* Dolff. Our investigations particularly concerned the potential of trophic exploitation of many microfungus strains present on the detritus of channels.

We intended to seek an answer to two questions, namely:
1) Do populations of two species of isopods co-occurring in the same biotope and two allopatrically occurring populations have a different potential trophic separation?
2) Do levels of trophic separation of the two species depend on the frequencies of the microfungal resources in nature?

Materials and methods

Asellus aquaticus and *Proasellus coxalis* are two naturally allopatric species of isopods. Characteristics of the biological cycle of both species have been thoroughly described by many authors (Chappuis 1949, Williams 1962, Vitagliano Tadini 1976).

Populations of the two species co-occurring in the same biotope were collected in a recess of Rio Galeria (Rome); allopatrically occurring populations of *A.*

aquaticus and *P. coxalis* instead were sampled from Rio Bufalotta (Rome) and Rio Fiora (Rome) respectively, in points where the streams form recesses. In these particular areas of the three channels, we could observe that *A.a.* and *P.c.* form most of the benthic biomass throughout the year, and their dispersion as far as the edges of the collection area is very limited. In this paper the pair of sympatric populations shall be termed *A.a. S + P.c. S* and their biotope *S*, the pair of allopatric populations *A.a. A – P.c. A* and their biotopes *A*.

We used only young animals born in the laboratory of females just collected in nature. To obtain population samples formed by individuals of the same size and to avoid contamination of the experimental environment, all the animals used were taken from the maternal pouch at early embryonic stages and kept in sterile culture until completely developed, according to a previously published technique (Rossi et al. 1975). The young animals (approx. 1 mm long) were distributed (25–30 ind.) in glass bowls 30 cm in diam. each containing 500 ml well water aerated and sterilized before use. Eighteen sets of 250–300 animals per species of each pair were separated; 16 sets were fed solely with fungi, one pure fungus strain per set (Diet A), two sets of each population were used as the control and for this purpose one was fed with sterilized detritus (Diet B) and the other with detritus enriched with microflora (Diet C). The suitability of each type of diet was evaluated on the basis of survival and body growth rate (variation in distance between the base of the antennae and the distal part of the telson) recorded every third day. Dead animals were removed and the water was changed every day. All experiments were carried out at a temperature of 16°C and under natural light conditions for 50 d.

The 16 fungi used (Diet A) were isolated by the dilution technique according to Bärlocher and Kendrick (1973) from packs of decaying leaves.

Monthly analyses of the detritus were carried out in each stream for six months (December–May) and the mean frequencies of the fungi were determined. Only the fungi always present at the period of sampling were singly cultured for 15 d at 16°C in malt extract broth. Ten pure fungus colonies (10 mm in diam.) were washed and offered to the animals. The colonies were replaced every third day.

The plant detritus offered (Diets B and C) consisted of dead leaves of *Alnus glutinosa*, *Salix alba* and *Quercus cerris*, collected near the habitats studied. The leaves were prepared in 3 g (dry wt) packs and sterilized in an autoclave; some of these were then offered in complete "asepsis" (Diet B). The remaining packs were incubated for 15 d at 16°C in an aqueous suspension of spores and hyphae of the 16 fungi offered. Packs so prepared were offered to the animals, one pack per bowl (Diet C).

The sterilization efficiency and the presence of microflora on leaves were verified by microbiological assay

of the 10 packs offered as Diet B and the 10 offered as Diet C.

The habitat

Some abiotic features of the three study areas were determined by standard methods (APHA et al. 1974) during animal samplings. As described in a previous publication the study areas have been artificially closed since 1950, the water flow is caused by irrigation pumps and the features of these biotopes studied are very similar (Rossi et al. 1980). Some differences can be found as regards microfungus populations. The value of the diversity index (Shannon-Wiener) is similar in the three biotopes (H′$_{(Bufalotta)}$ = 2.43; H′$_{(Fiora)}$ = 2.34; H′$_{(Galeria)}$ = 2.05), but the frequencies of fungi are more similar in the two biotopes (Bufalotta and Fiora) where the two species of isopods live alone, than in the "S" biotope and the two "A" biotopes (Tab. 1).

Results

A microbiological analysis of leaf packs showed the total asepsis of packs offered in Diet B and the microbial development on inoculated packs offered in Diet C. Detritus without microflora is not a suitable food to satisfy the energy requirements of the young animals; all individuals to which it was offered as the only food source refused it (the leaves were not skeletonized) and died within the first 15 d of the experiment (Tabs 2 and 3).

The various fungi offered as the sole food source are nutritionally adequate. In fact: the *A.a. S* show a survival which is higher than or equal to the control (leaves as food), for ten out of sixteen microfungus species offered; the *P.c. S* survive to the same or a greater extent than the control for eight strains (Tab. 4a), only four of which (*C. aquatica, A. awamori, C. herbarum, P. cyclopium*) are also suitable for the other species (n.s. in Tab. 2). Hence, *A.a. S* prevails over *P.c. S* as regards the exploitation of 6 of its 10 favourite strains, while *P.c. S* prevails over *A.a. S* as regards the exploitation of four of its eight favourites (Tab. 2, Fig. 1).

The *A.a. A* survive like the respective control animals with seven of sixteen fungi offered. The same applies to the *P.c. A* (Tab. 4b). Five of the seven fungi (*A. strictum, C. aquatica, P. cyclopium, P. uncialicola, T. pseudokoningii*) are likewise exploited by both species (n.s. in Tab. 3).

All survivors of the four populations fed on fungi show a greater average body growth than control animals fed only on dead leaves (Tabs 2 and 3).

Considering the whole set of 16 microfungi, the comparison of the distribution of survivors between the two species is significantly different only for sympatric population (*A.a. S, P.c. S*). The intraspecific compari-

Tab. 1. Monthly frequencies ($\bar{x}$% ± 2 s.e. in parenthesis) of 16 species of fungi present throughout the study in the three biotopes.

Stream	*Pen. cyclopium*	*Clad. herbarum*	*Asp. awamori*	*Fus. oxysporum*	*Clav. aquatica*	*Acr. strictum*	*Flag. curvula*	*Ang. longissima*	*Trich. pseudokoningii*	*Pho. uncialicola*	*Alt. tenuis*	*Muc. mucedo*	*Trich. harzianum*	*Asp. niger*	*Fus. solanii*	*Hum. grisea*
"S" Galeria (*A. aquaticus*) (*P. coxalis*)	27.10 (2.29)	25.40 (2.10)	16.00 (1.60)	8.50 (1.05)	5.20 (0.73)	3.97 (0.35)	2.91 (0.40)	2.53 (0.40)	2.02 (0.60)	1.86 (0.29)	1.56 (0.90)	1.13 (0.89)	0.58 (0.20)	0.54 (0.25)	0.46 (0.12)	0.40 (0.23)
"A" Bufalotta (*A. aquaticus*) alone	9.27 (1.38)	15.50 (0.68)	4.89 (0.80)	4.11 (0.50)	13.2 (1.50)	14.20 (1.10)	1.12 (0.23)	2.21 (0.50)	12.20 (1.00)	4.50 (0.50)	0.60 (0.25)	0.16 (0.09)	2.01 (0.60)	1.99 (0.44)	6.36 (0.66)	7.64 (0.57)
"A" Fiora (*P. coxalis*) alone	7.50 (1.65)	14.70 (1.75)	5.88 (0.75)	5.20 (0.40)	16.30 (1.70)	15.10 (1.05)	2.00 (0.50)	3.21 (0.55)	16.40 (1.10)	3.55 (0.80)	0.37 (0.20)	0.43 (0.20)	4.12 (0.75)	3.07 (0.33)	2.01 (0.21)	0.10 (0.08)

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Tab. 2. Sympatric populations. Survival and body growth of undifferentiated young *A. aquaticus* and *P. coxalis,* born by females collected from the same biotope (Galeria), to whom 18 different types of food were offered for 50 d. * – Significance of the difference between the two species, χ^2 test; ** – Significance of the difference in growth compared to the control animals fed with leaves, t-test; § = p < 0.01; n.s. = not significant.

Source of food		No. animals at start	Survivors no.	%	*	Body length (mm) x ± 2 s.e.	**
P. cyclopium ...	A.a.	288	217	75.3		5.64±0.27	§
	P.c.	206	180	87.4	n.s.	4.39±0.26	§
C. herbarum ...	A.a.	295	204	69.1		5.05±0.16	§
	P.c.	200	128	64.0	n.s.	3.51±0.13	§
A. awamori	A.a.	298	258	86.6		4.18±0.18	§
	P.c.	278	212	76.2	n.s.	3.75±0.27	§
F. oxysporum ..	A.a.	280	133	47.5		3.99±0.18	§
	P.c.	250	116	46.4	n.s.	4.63±0.14	§
C. aquatica	A.a.	260	169	65.0		4.34±0.15	§
	P.c.	230	196	85.2	§	3.86±0.25	§
A. strictum	A.a.	300	141	47.0		3.49±0.24	§
	P.c.	290	209	72.1	§	4.32±0.18	§
F. curvula	A.a.	276	242	87.7		4.27±0.20	§
	P.c.	266	34	12.8	§	3.14±0.26	§
A. longissima ..	A.a.	287	262	91.3		4.56±0.18	§
	P.c.	284	85	29.9	§	3.97±0.22	§
T. pseudo-koningii	A.a.	290	113	38.9		3.48±0.21	§
	P.c.	260	232	89.2	§	3.65±0.16	§
P. uncialicola ..	A.a.	270	155	57.4		3.83±0.24	§
	P.c.	282	18	6.4	§	4.11±0.31	§
A. tenuis	A.a.	270	216	80.0		4.18±0.13	§
	P.c.	290	54	18.4	§	3.33±0.31	§
M. mucedo	A.a.	260	164	63.1		3.97±0.10	§
	P.c.	270	36	13.3	§	3.85±0.26	§
T. harzianum ..	A.a.	276	106	38.4		4.35±0.33	§
	P.c.	274	238	86.9	§	4.37±0.34	§
A. niger	A.a.	266	89	33.5		4.11±0.16	§
	P.c.	278	241	86.7	§	3.90±0.20	§
F. solanii	A.a.	285	264	92.6		4.77±0.22	§
	P.c.	294	0	0.0	§	– –	
H. grisea	A.a.	286	233	81.5		4.00±0.23	§
	P.c.	200	0	0.0	§	– –	
Leaves	A.a.	430	314	73.0		2.83±0.11	
	P.c.	360	256	71.1	n.s.	2.66±0.14	
Sterile leaves ..	A.a.	286	0	0.0		– –	
	P.c.	226	0	0.0		– –	

Tab. 3. Allopatric populations. Survival and body growth of undifferentiated young *A. aquaticus* and *P. coxalis,* born by females collected from two separate biotopes (Bufalotta and Fiora respectively), to whom 18 different types of food were offered for 50 d. * – Significance of the difference between the two species, χ^2 test; ** – Significance of the difference in growth compared to the control animals fed with leaves, t-test; § = p < 0.01; n.s. = not significant.

Source of food		No. animals at start	Survivors No.	%	*	Body length (mm) x ± 2 s.e.	**
P. cyclopium ...	A.a.	225	146	64.9		3.55±0.15	§
	P.c.	253	187	73.9	n.s.	3.33±0.10	§
C. herbarum ...	A.a.	280	157	56.1		4.67±0.16	§
	P.c.	250	165	66.0	n.s.	3.63±0.09	§
A. awamori	A.a.	320	147	45.9		3.63±0.21	§
	P.c.	254	129	50.8	n.s.	3.22±0.16	§
F. oxysporum ..	A.a.	290	134	46.2		3.15±0.18	n.s.
	P.c.	250	130	52.0	n.s.	3.77±0.11	§
C. aquatica	A.a.	260	174	66.9		4.67±0.21	§
	P.c.	255	180	70.6	n.s.	3.67±0.11	§
A. strictum	A.a.	280	196	70.0		3.66±0.14	§
	P.c.	260	182	70.0	n.s.	4.11±0.11	§
F. curvula	A.a.	248	99	39.9		3.55±0.18	§
	P.c.	250	125	50.0	n.s.	3.70±0.21	§
A. longissima ..	A.a.	280	92	32.9		4.18±0.12	§
	P.c.	225	59	26.2	n.s.	3.71±0.20	§
T. pseudo-koningii	A.a.	280	171	61.0		3.45±0.18	§
	P.c.	260	192	73.8	n.s.	4.00±0.11	§
P. uncialicola ..	A.a.	218	146	67.0		4.28±0.11	§
	P.c	240	144	60.0	n.s.	4.10±0.15	§
A. tenuis	A.a.	285	53	18.6		3.25±0.18	§
	P.c.	261	46	17.6	n.s.	3.75±0.14	§
M. mucedo	A.a.	280	42	15.0		4.11±0.31	§
	P.c.	250	52	20.8	n.s.	3.21±0.14	§
T. harzianum ..	A.a.	250	62	24.8		3.77±0.23	§
	P.c.	246	163	66.3	§	4.01±0.21	§
A. niger	A.a.	270	54	20.0		2.93±0.18	n.s.
	P.c.	296	148	50.0	§	3.71±0.13	§
F. solanii	A.a.	277	180	65.0		4.27±0.20	§
	P.c.	280	0	0.0	§	– –	
H. grisea	A.a.	256	183	71.4		3.87±0.12	§
	P.c.	244	0	0.0	§	– –	
Leaves	A.a.	300	210	70.0		2.81±0.16	
	P.c.	300	210	70.0	n.s.	2.30±0.12	
Sterile leaves ..	A.a.	200	0	0.0		– –	
	P.c.	160	0	0.0		– –	

sons show different distributions of survivors in *A.a. S – A.a. A* and similar distributions in *P.c. S – P.c. A* (Tab. 5).

The greatest trophic separation between *A.a. S* and *P.c. S* is observed in mycetes at the lowest frequencies in the *S* biotope. A significant inverse correlation between the difference of survivors of the two species on each fungus and the percentage of the latter in the biotope is verified r = –0.7216, n = 16, p < 0.01 (Fig. 1). Instead, both for *A.a. A* and for *P.c. A* a significant direct correlation between amount of resource in the respective environment and percentage of individuals able to exploit this is verified (*A.a. A*: r = 0.7691, n = 16, p < 0.01; *P.c. A*: r = 0.7330, n = 16, p < 0.01) (Fig. 1).

Discussion

This study is based on laboratory rather than field observations. Therefore we can reasonably assume that other food resources besides those offered, and other factors besides food can influence isopod populations in nature. However, in the context of the present study, we wish to point out that 1) populations of *A. aquaticus* and *P. coxalis* from sympatry show a much greater potential trophic differentiation than populations of the two species occurring in allopatry; 2) potential trophic separation of the two species from sympatry, on a given resource, is inversely proportional to the frequency of the resource itself in the natural biotope.
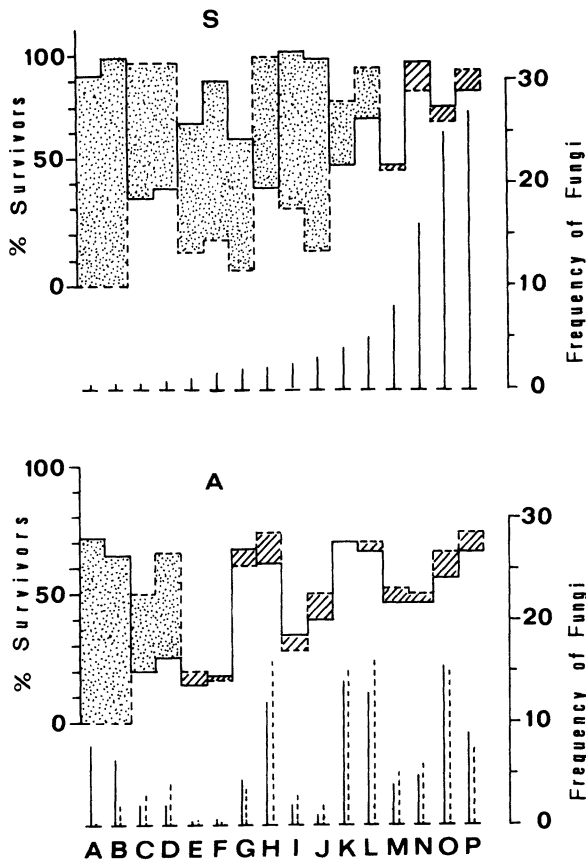
Fig. 1. Survival of sympatric (S) and allopatric (A) populations of *A. aquaticus* (———) and of *P. coxalis* (– – –) when they utilize as only food source each of 16 fungi represented by capital letters (A = *Hum. grisea* and P = *Pen. cyclopium*, see Tab. 2). The frequency of each fungus in the biotope of sympatry and in the biotopes where *A.a.* (———) and *P.c.* (– – –) live alone is shown. Dotted and dashed areas represent respectively significant (p < 0.01) and not significant differences between survivals of the two species on each resource of food.

The first point arises from the evidence that young individuals of *A.a.* and *P.c.* sympatric populations have a potential overlap in the use of only 25% of the tested microfungal resources. On the other hand, in allopatry young *A.a.* and *P.c.* individuals have a potential overlap in the use of as much as 75% of the same set of trophic resources. We observed a similar trophic differentiation in another co-occurring pair of isopod populations (Rossi and Fano 1979) and this supports our present results. However, food specialization is an ecological isolating strategy often observed in nature. Physiological rather than morphological modifications, like those observed by us, are often the basis of the niche separations (Fellows and Heed 1972, Calow and Calow 1975).

The strong similarity of the two species from allopatry appears to be an understandable consequence of food strategies peculiar to the two species. In other words,

they can exploit to a greater extent the most common fungi of the respective biotopes. In fact, the variable "resource frequency – animal survival" are correlated. Furthermore the frequencies of various microfungi are very similar in biotopes where *A.a.* and *P.c.* live alone and the only fungi for which the two allopatric populations are differentiated are those having a different frequency in the two respective biotopes. Density-dependent exploitation is a foraging strategy very common in animals (Fenchel 1975, Werner and Hall 1979), and this feature is also not completely lacking in the two species from sympatry. In fact the most frequent fungus in the *S* biotope can be exploited by almost the whole population of each species.

The different trophic suitability of the various fungi for individuals of a single population or of a single fungus for individuals of different populations cannot be attributed to the different ages of the colonies offered. The latter were replaced every third day with pure colonies of the same age, so that also differential contamination by protozoa and bacteria were avoided. Such contamination is often indicated as a modifier of nutritional suitability (Nikolei 1960, cit. by Bärlocher and Kendrick 1973, Marcus and Willoughby 1978).

Also phenomena related to the age of the animals should not matter here, since the animals in all tested samples were of the same age. In our opinion, variabilities observed in the populations are probably cases of polymorphism based on metabolic differences and derive from the presence of many genotypes in each population having different trophic needs or immunotoxic capacities (Bärlocher 1979). Is well known that the fungi have peculiar biochemical differences both as concerns vitamins and proteins and toxins (Swift 1976). On the other hand, the survival of even a few individuals on a particular resource which can permit them a regular development shows the existence, in each species, of genotypes fit for a profitable use of that resource. This opinion is also supported by Christensen's results (1977) concerning a correspondence between the level of amylasic polymorphism in two populations of *A. aquaticus* and the relative trophic substrate. The author hypothesizes a trophic partitioning through a frequency-dependent selection of the various genotypes.

The differences found in conspecific populations both of *A.a.* and of *P.c.* may be ascribed to this fact. In fact the *S*. populations show a higher frequency of phenotypes fit for the exploitation of the fungi less used in allopatric conditions.

The fact that *A.a.* populations are significantly differentiated as compared to *P.c.* populations is very probably due to the greater genetic potential of the former: *A.a.* has a broader distribution than *P.c.* and its characteristics are more euryecological and plastic (Vitagliano Tadini 1976, Christensen 1977, Rossi and Fano 1979). On the other hand, cases of niche shift in only one of the two co-occurring species with respect to an

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Tab. 4a. Sympatric populations. Significance levels of the differences between the number of survivors of the same species on each food resource offered for 50 d to young *Asellus aquaticus* (the left arrow in each pair) and *Proasellus coxalis* (right arrow). The arrows point to the higher value. χ^2 test, arrows = 95% confidence level, − = not significant.

	Acr. strictum	Alt. tenuis	Ang. longissim.	Asp. awamori	Asp. niger	Clad. herbar.	Fla. curvula	Fus. oxyspor.	Fus. solanii	Hum. grisea	Muc. mucedo	Pen. cyclopium	Pho. uncialicola	Clav. aquatica	Tric. harzianum	Tric. pseudoko.
Alt. tenuis	←↑	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ang. longissima	←↑	←←	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asp. awamori	←−	←←	−←	.	.	.	.	.	.	.	.	.	.	.	.	.
Asp. niger	↑←	↑←	↑←	↑←	.	.	.	.	.	.	.	.	.	.	.	.
Clad. herbarum	←−	↑←	↑←	↑↑	←↑	.	.	.	.	.	.	.	.	.	.	.
Fla. curvula	←↑	←−	−↑	−↑	←↑	←↑	.	.	.	.	.	.	.	.	.	.
Fus. oxysporum	−↑	↑←	↑←	↑↑	←↑	↑↑	↑←	.	.	.	.	.	.	.	.	.
Fus solanii	←↑	←↑	−↑	←↑	←↑	←↑	←↑	←↑	.	.	.	.	.	.	.	.
Hum grisea	←↑	−↑	↑↑	−↑	←↑	←↑	↑↑	←↑	↑←	.	.	.	.	.	.	.
Muc. mucedo	←↑	↑−	↑−	↑↑	←↑	−↑	↑−	←↑	↑←	↑←	.	.	.	.	.	.
Pen cyclopium	←←	−←	−↑	↑−	←−	−←	↑←	←←	↑←	−←	←←	.	.	.	.	.
Pho. uncialicola	←↑	↑↑	↑↑	↑↑	←↑	↑↑	↑↑	←↑	↑←	↑←	−←	↑↑	.	.	.	.
Pho. uncialicola	←↑	↑↑	↑↑	↑↑	←↑	↑↑	↑↑	←↑	↑←	↑←	−←	↑↑	.	.	.	.
Clav. aquatica	←←	↑←	↑←	↑←	←−	−←	↑←	←←	↑←	↑←	−←	↑−	−←	.	.	.
Tric. harzianum	↑←	↑←	↑↑	↑←	−−	↑←	↑←	↑←	↑←	↑←	↑←	↑−	↑←	↑−	.	.
Tric. pseudokoningii	↑←	↑←	↑←	↑←	−−	↑←	↑←	↑←	↑←	↑←	↑←	↑−	↑←	↑↑	−	.
Leaves	←−	−←	↑←	↑−	←↑	−−	↑←	←←	↑←	−←	−←	−↑	←←	−↑	←↑	←↑

Tab. 4b. The same as for Tab. 4a, but for allopatric populations.

	Acr. strictum	Alt. tenuis	Ang. longissima	Asp. awamori	Asp. niger	Clad. herbarum	Clav. aquatica	Flag. curvula	Fus. oxysporum	Fus. solanii	Hum. grisea	Muc. mucedo	Pen. cyclopium	Pho. uncialicola	Tric. hartianum	Tric. pseudoko.
Alt. tenuis	↑↑	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ang. longissima	↑↑	−−	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asp. awamori	↑↑	←←	−←	.	.	.	.	.	.	.	.	.	.	.	.	.
Asp. niger	↑↑	−←	−←	←−	.	.	.	.	.	.	.	.	.	.	.	.
Clad. herbarum	↑−	←←	←←	←←	←←	.	.	.	.	.	.	.	.	.	.	.
Clav. aquatica	−−	←←	←←	←←	←←	←−	.	.	.	.	.	.	.	.	.	.
Flag. curvula	↑↑	←←	−←	−−	←−	↑↑	↑↑	.	.	.	.	.	.	.	.	.
Fus. oxysporum	↑↑	←←	−←	−−	←−	↑↑	↑↑	−−	.	.	.	.	.	.	.	.
Fus. solanii	−↑	←↑	←↑	←↑	←↑	←↑	−↑	←↑	←↑	.	.	.	.	.	.	.
Hum. grisea	−↑	←↑	←↑	←↑	←↑	←↑	−↑	←↑	←↑	−−	.	.	.	.	.	.
Muc. mucedo	↑↑	−−	↑−	↑↑	−↑	↑↑	↑↑	↑↑	↑↑	↑←	↑←	.	.	.	.	.
Pen cyclopium	−−	←←	←←	↑↑	←←	−−	−−	←←	←←	−←	−←	←←	.	.	.	.
Pho. uncialicola	−−	←←	←←	←−	←−	−−	−−	←−	←−	−←	−←	←←	−−	.	.	.
Tric. harzianum	↑−	−←	−←	←←	−←	↑−	↑−	−−	↑←	↑←	↑←	←←	↑−	↑−	.	.
Tric. pseudokoningii	↑−	←←	←←	←←	←←	−−	−−	←←	←←	−←	↑←	←←	−−	−−	←−	.
Leaves	−−	←←	←←	←←	←←	←−	−−	←←	←←	−←	−←	←←	−−	−−	←−	−−

Tab. 5. Analysis of variance for numbers of *A. aquaticus* and *P. coxalis* populations (coexisting and occurring in allopatry) fed on the same diet-series.

	Degrees of freedom	Sums of squares	F-statistic	Significance of F
Occurring in sympatry *A.a.S – P.c.S*	30	27825	2.89645	p <0.001
Occurring in allopatry *A.a.S – P.c.A*	30	16033	0.01812	n.s.
Intraspecific *A.a.S – A.a.A*	30	14865	6.40536	p < 0.01
Intraspecific *P.c.S – P.c.A*	30	29172	0.02331	n.s.

allopatric situation are common in the literature (Fenchel 1975).

Our data do not allow for further speculations on the subject. However cases of variability in exploiting fungi as trophic resources have been also observed in populations of other animal species such as *Gammarus pseudolimnaeus* (Bärlocher and Kendrick 1973), in *Ceratitis capitata* (Cavicchi and Zaccarelli 1974) and in many species of *Drosophila* (Gilpin 1974, Kimura 1980) where individual variability in food selection causes polyphagy, a feature of the whole population and subsequently of the whole species.

We believe that the trophic variability found in these isopod populations allows them to remain in their own biotope and implies a potential against manifestations of competitive exclusion. Furthermore, the trophic differentiation of the two species appears to be a consequence of competitive coevolution rather than of an adaptation to the physical environment. In effect, although many factors may influence animal nutrition and many variables of the biotopes studied are not yet known, we may assume that the presence of both or only one species is the most relevant difference between the biotopes. Active migration should be limited by structure of the habitats and probably the same population have co-occurred for many years. Furthermore, the different frequency with which some resources occur in *A* and *S* biotopes does not seem to be responsible for changes in potentials of conspecific populations, living alone or with the other species. There are cases where resource frequency changes while survival remains identical (e.g. *C. herbarum* for *A.a.* and *P. cyclopium* for *P.c.*), and, viceversa, cases where the frequency is identical while survival of populations is different (e.g. *F. oxysporum* for *A.a.*). We do not believe that this result was influenced by microfungus frequency determination techniques. It would be very strange, in the case of analytical inaccuracies, to find that the trophic differentiation of *A.a.* and *P.c.* from sympatry is proportionally greater on microfungus resources less available in the environment. This also supports a coevolutionary interpretation of our results, since the inverse correlation between strength of competition and trophic availability is now accepted (MacArthur 1970). Moreover, whenever we observe a variation of trophic suitability of a resource in conspecific populations (from allopatry to sympatry) the variation is to the advantage of

the prevailing species in that resource in conditions of allopatry. This leads us to believe in a favourable selection of that of the two species having the highest number of individuals fit to exploit a certain resource already in pre-interactive conditions.

In conclusion, our results can suggest a possible effect of co-occurrence on character displacement shown by co-occurring populations and support the theory of coevolutionary trophic partitioning between the two species, and emphasize the role of microfungi in detritivorous animal coexistence relationships.

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