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Species-specific utilization of food sources by sympatric woodlice (Isopoda: Oniscidea)

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Summary

1. In long-term laboratory studies, the influence of different food materials on parameters of population dynamics was compared in the sympatric woodlice, *Porcellio scaber* and *Oniscus asellus*, as a measure of interspecific differences in the utilization of food.

2. Freshly fallen leaf litter of different tree species had been acidified and microbially inoculated prior to the experiments. By analysing the influence of pH level, density and activity of litter-colonizing microbiota and several physico-chemical characteristics of the leaf litter, we obtained information on those factors that determine food quality.

3. The studied species responded similarly to different leaf litter species in that both *P. scaber* and *O. asellus* performed better on litter with low C:N ratio. Overall, both isopod species reproduced more successfully on litter with higher pH levels, containing half the levels of tannins and other phenolics.

4. Interspecific differences were obvious with respect to the significance of litter-colonizing microbiota, and the dependence of juveniles on particular food parameters. While the performance of adult *P. scaber* was influenced by both litter-colonizing microbiota and physico-chemical characteristics of the leaf litter, adult *O. asellus* were influenced by leaf litter characteristics, but not by litter-colonizing microbiota. Juvenile mortality was affected by the tested food parameters in *O. asellus*, but not in *P. scaber*. Growth rates of juveniles of both species were influenced by physico-chemical characteristics of the leaf litter. Additionally, leaf litter microbiota had a significant influence on growth rates in juvenile *P. scaber*, but not in juvenile *O. asellus*.

5 Reasons for, and consequences of, similarities and differences between the observed sympatric species, and intraspecific differences between ontogenetic stages, are important aspects of soil ecology and may help explain the sympatric coexistence of two species belonging to the same guild of saprophagous soil animals.

Key-words: coexistence, leaf litter microbiota, *Oniscus asellus*, population dynamics, *Porcellio scaber*, terrestrial isopods.

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Introduction

From coexistence, limitations to the overlap of resource utilization by sympatric species can be predicted. Previous studies on sympatric saprophagous invertebrates in aquatic systems suggested that differential food utilization is an important factor allowing for coexistence (e.g. Arsuffi & Suberkropp 1989; Graça, Maltby & Calow 1993). By contrast, it has been accepted for decades that members of the guild of saprophagous soil animals exhibit similar nutritional requirements, being represented by similar feedings preferences (summarized in: Topp 1981; Petersen & Luxton 1982; Dunger 1983). When considering nutritional requirements, the main areas examined have been food preference, consumption and assimilation of food, and growth. In contrast to these short-term studies, long-term investigations of population dynamics allow integration of the perfor-

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mance processes on a population as well as an individual level. Thus, these studies may elucidate those factors that differentially determine food quality in sympatric species belonging to the same guild.

In populations of terrestrial isopods (Isopoda: Oniscidea), climatic factors have been shown to influence natality and mortality (summarized in Warburg, Linsenmair & Bercovitz 1984). Since the number of offspring is correlated with the size of females (Standen 1973; Sutton *et al*. 1984; Hassall & Dangerfield 1990), and hence, with nutrition (Merriam 1971; Sunderland, Hassall & Sutton 1976), population dynamics may be influenced by nutritional conditions. Food shortage has been shown to increase mortality in *Armadillidium vulgare* (Latr.) (Ganter 1984), leading to lower numbers of larger offspring (Brody & Lawlor 1984), and the food material also influences the population dynamics of this species (Merriam 1971; Rushton & Hassall 1983a; 1987). Mortality and reproductive success of *Porcellio scaber* Latr. mainly depend on microbial colonization of leaf litter (Zimmer & Topp 1997a). No comparable information is available for *Oniscus asellus* L. that is sympatric with that *P. scaber* (e.g. Beyer 1964; Zimmer & Topp 1999). Since ingested microbiota are digested by both *O. asellus and P. scaber* (Coughtrey *et al*. 1980; Gunnarsson & Tunlid 1986; Zimmer & Topp 1998a), the biomass of litter-colonizing microbiota may be a determinant of food quality in both species. Degradation of cellulose and oxidation of phenolic compounds of the leaf litter have been demonstrated in both species (Hartenstein 1964; Neuhauser & Hartenstein 1976; Zimmer & Topp 1998a,b; Zimmer 1999a). Thus, nutritional requirements may be similar. The present study was carried out to compare these sympatric woodlouse species with respect to species-specific similarities and differences in the effects of different food materials on growth, reproduction and mortality, resulting in changes in population size.

Materials and methods

FOOD

Freshly fallen leaf litter of three palearctic tree species, alder (*Alnus glutinosa* (L.) Gaertn.), birch (*Betula pendula* Roth), and oak (*Quercus robur* L.), was collected in the vicinity of Cologne, Germany, in the autumn of 1993, and was air-dried and stored in the laboratory to prevent changes in the chemical composition due to microbial decomposition processes (cf. Zimmer & Topp 1997a). Prior to the experiment, the leaf litter was experimentally conditioned by soaking in sulphurous acid of either pH 3·0 or pH 5·0 for 1 week, and by subsequent microbial inoculation (21 days) in a pool of mixed leaf litter freshly collected in the field (Zimmer & Topp 1997a). Experimental pH manipulation is known to cause changes in physico-chemical characteristics of the leaf litter that, in turn, result in food sources with different levels of microbial density and activity after inoculation (Zimmer & Topp 1997a). Thus, six leaf litter materials (*al*-, *be*- and *qu*-, for alder, birch and oak, respectively; *-3* and *-5*, for pH 3- and pH 5-manipulated leaf litter, respectively) with different chemical, physical and microbiological properties were obtained (Table 1; cf. Zimmer & Topp 1997a) that served as food for *P. scaber* and *O. asellus*.

The pH level of the leaf litter was determined in the supernatant of a suspension of 50 mg homogenized leaf litter material in 1 mL 3 M KCl. Microbial activity of the leaf litter was estimated in terms of cellulase activity (glucose release) and respiration (CO_2 evolution) as described by Skambracks & Zimmer (1998). The same samples were subsequently used for determining the density of bacteria, yeasts

Table 1. Microbiological, physical and chemical characteristics of leaf litter used as food materials for *Porcellio scaber* and *Oniscus asellus*. Data are given as median ± median absolute deviation of monthly measurements (1994–97; $n = 215$)

		Alnus glutinosa		*Betula pendula*		*Quercus robur*	
pH manipulation		3·0	5·0	3·0	5·0	3·0	5·0
pH level		3·5 ± 0·3	5·9 ± 0·3	3·3 ± 0·2	5·5 ± 0·3	3.1 ± 0·4	5·6 ± 0·3
Bacterial numbers	10^{10} cells g^{-1}	4·7 ± 0·3	3·5 ± 0·2	1·9 ± 0·5	2·3 ± 0·1	1·9 ± 0·2	4·4 ± 0·9
Cellulolytic activity	μg Glc $(g\ h)^{-1}$	220 ± 90	700 ± 95	330 ± 92	230 ± 99	240 ± 91	340 ± 81
Respiratory activity	μg CO_2 $(g\ h)^{-1}$	89 ± 11	127 ± 13	49 ± 12	50 ± 8	88 ± 10	44 ± 6
Water content	%	27 ± 4	30 ± 4	40 ± 1	40 ± 4	37 ± 7	37 ± 5
Physical strength	g mm^{-2}	13 ± 2	12 ± 2	19 ± 4	22 ± 3	58 ± 5	41 ± 9
Phenolics	mg g^{-1}	27 ± 1	16 ± 1	30 ± 1	11 ± 1	36 ± 1	15 ± 1
Hydrolysable tannins	mg g^{-1}	48 ± 5	34 ± 3	8 ± 2	2 ± 1	29 ± 2	14 ± 1
Condensed tannins	mg g^{-1}	13 ± 1	10 ± 1	16 ± 1	13 ± 1	10 ± 2	8 ± 1
Nitrogen	mg g^{-1}	35 ± 4	32 ± 3	19 ± 2	17 ± 2	16 ± 3	16 ± 2
C:N ratio		15 ± 1	16 ± 1	27 ± 2	29 ± 2	30 ± 1	28 ± 2
Cellulose	mg g^{-1}	444 ± 17	421 ± 7	468 ± 5	468 ± 8	507 ± 13	507 ± 9
Lignins	mg g^{-1}	178 ± 11	189 ± 7	151 ± 13	156 ± 9	284 ± 11	298 ± 12

and fungal propagules, referred to as 'bacterial numbers', as described by Francisco, Mah & Rabin (1973). Physico-chemical characteristics of the leaf litter were described through water content (gravimetrically, 24 h, 60 °C), physical strength (modified after Tanton 1962), the content of phenolics and hydrolysable and condensed tannins (Zimmer 1997), the C:N ratio (N: Kjeldahl method, Gerhardt, Bonn, Germany; C: Total Organic Carbon analyser, Ströhlein-Instruments, Kaarst, Germany), and the content of cellulose and lignins (Zimmer 1999b).

WOODLICE

Pre-adult individuals of *Porcellio scaber* and *Oniscus asellus* were collected in a mixed alder–poplar forest near Cologne, Germany, during autumn 1993 and 1994, respectively. Because they were collected at the same site, the experimental sets of isopods represented biogeographically similar populations *sensu* Sachs (1988).

During their first winter in the laboratory, isopods were kept at 5 °C and 8 h L:16 h D in translucent plastic containers, the bottoms of which were covered with a 20-mm layer of sieved (2 mm) sandy top soil from the site where the isopods had been captured. A mixture of leaf litter from different tree species (alder, birch, maple, oak, poplar) served as food. Prior to the experiments, temperature and photoperiod were changed stepwise to 15 °C and 16 h L:8 h D.

EXPERIMENTAL DESIGN

In March 1994, two populations of 10 pre-adult females [(1·3 ± 0·2) mm head width] and five pre-adult males [(1·3 ± 0·3) mm head width] of *P. scaber*, were initiated on each of the above-mentioned food materials ('*al3*', '*al5*', '*be3*', '*be5*', '*qu3*', '*qu5*'). After four reproductive seasons, the experiment was terminated in October 1997. Thus, each food material was represented by two replicate data sets with four repeated measures on reproduction, mortality and growth of isopods. Overall, 48 reproductive phases were observed in these populations.

In March 1995, three populations of five adult females [(1·8 ± 0·3) mm] and three adult males [(1·8 ± 0·4) mm] of *O. asellus*, were initiated on each of the above-mentioned food materials. After three reproductive seasons, the experiment was terminated in October 1997. Thus, each food material was represented by three replicate data sets with three repeated measures on reproduction, mortality and growth of isopods. Overall, 54 reproductive phases were observed in these populations.

The initial density of *O. asellus* and *P. scaber* corresponded to 200 and 375 isopods m^{-2}, respectively. These densities are close to those at different localities in the vicinity of Cologne, where on average *P. scaber* is slightly more abundant (M. Zimmer, unpublished). Differences in initial population densities may lead to interspecific differences in density-dependent processes, but we expected the size of the experimental populations to be regulated according to the nutritive conditions, determining the carrying capacity of the artificial environment. Since individuals were assigned to the experimental treatments randomly, the initial populations did not differ from each other with respect to individual size (head width; $P > 0{\cdot}3$; *H*-test). Hence, the samples had equal size representation, and thus, represented structurally similar populations *sensu* Sachs (1988).

During the experiments, populations were kept in translucent plastic containers (200 × 200 mm) with a plaster of Paris floor to maintain humidity (cf. Zimmer & Topp 1997a) and to prevent geophagy. Broken pieces of terra cotta as well as the loose layers of leaf litter served as shelters. Leaf litter was provided in surplus and was replaced monthly by freshly conditioned litter. Faeces were not removed from the containers to allow for coprophagy (cf. Hassall & Rushton 1982, 1985; Helden & Hassall 1998). Further, corpses of dead isopods remained in the containers to serve as supplementary food source, but were removed as soon as they were covered with mould.

Once a year (in November), populations were transferred to fresh containers with an oven-dried (60 °C, 48 h) and re-wetted plaster flooring to prevent extensive development of mould inside the containers. To provide constant nutritive conditions, the leaf litter, being partially covered with faeces, but not the layer of faeces covering the plaster flooring, was transferred together with the isopods.

From March to November, temperature (15 °C) and photoperiod (16 h L:8 h D) were kept constant. During December, temperature was lowered to 10 °C, and photoperiod was changed stepwise (four steps of 1 week each) to 8 h L:16 h D. In January, isopods were kept at 5 °C (8 h L:16 h D). During February, temperature was increased to 10 °C again, and photoperiod was adjusted stepwise to 16 h L:8 h D.

During the reproductive season (May–October), experimental populations were checked twice a week for freshly released mancae that were quantified immediately (max. 4 days) after hatching. Once a month, a census was performed by sexing adults, counting juveniles, pre-adults, and adult males and females, and checking females for gravidity. Additionally, every 3 months, the size (head width: Sutton 1968; Sunderland *et al.* 1976) of juvenile individuals was measured under a stereomicroscope with an accuracy of ± 0·02 mm to obtain data on growth rates in both *P. scaber* and *O. asellus*. Due to the appearance of external sexual characters (gonopods) in males, juvenile *P. scaber* and *O. asellus* of 1·0 mm and 1·1 mm head width, respectively,

were considered pre-adult. However, juveniles and pre-adults were pooled as 'juveniles' in our analyses, because neither contribute to reproduction.

It was not possible to determine the size of marked individuals, so mean juvenile growth rates (μm per month) were calculated from the data on mean head width (H) of juveniles. We also included the sizes of freshly maturated individuals until the next reproductive season led to freshly released mancae. Although freshly released mancae may result in an underestimation of growth rates of older juveniles, the dates of measurements (January, April, July, October) proved to largely eliminate this experimental problem. In only 17 (out of 48) and 9 (out of 54) reproductive phases of *P. scaber and O. asellus*, respectively (see above), could the growth rates have been underestimated due to reproduction between July and October (cf. Figures 1 and 3). This underestimation mainly occurred in populations with extensive reproduction and high juvenile growth rates, and thus resulted in a conservative determination of food-induced differences in growth rates.

POPULATION DYNAMICS

Parameters of population dynamics were estimated discontinuously. In our model, the change in population size from one reproductive season to the next one (= 1 year) is given by

$$N_{t+1} - N_t = RN_t - M\,(N_t + RN_t) \qquad \text{eqn 1a}$$

where R is the rate of reproduction, and M is the rate of mortality. RN_t is the term of reproduction, and $M(N_t + RN_t)$ is the term of mortality. Thus, population size after 1 year is

$$N_{t+1} = N_t + RN_t - M\,(N_t + RN_t)$$
$$= (N_t + RN_t)\,(1 - M) \qquad \text{eqn 1b}$$

where $(N_t + RN_t)$ is the maximal population size during the reproductive period, $N_{\max}$.

$$N_{\max} = N_t + RN_t \qquad \text{eqn 1c}$$

includes adults (N_t) and the total number of recruits to the population due to reproduction

$$RN_t = N_{\mathrm{F}} \qquad \text{eqn 1d}$$

The total number of offspring, N_{F}, was determined by counting freshly released mancae immediately (max. 4 days; see above) after hatching, in order to prevent an underestimation of reproduction due to high mortality of mancae. N_{F} mainly depends on the number of females, rather than males. Thus, the rate of reproduction was calculated in relation to the number of mature females (cf. Miller & Cameron 1983):

$$R^{\mathrm{f}} = \frac{N_{\mathrm{F}}}{N_t^{\mathrm{f}}} \qquad \text{eqn 2}$$

where $N_{\mathrm{t}}^{\mathrm{f}}$ is the number of mature females in N_t.

Total mortality is determined by juvenile mortality, M^{juv}, and adult mortality, M^{ad}, that were calculated independently in our study. According to previous studies on maturation in terrestrial isopods (M. Zimmer, unpublished), individuals of *P. scaber* and *O. asellus* were considered adult when having a head size of 1·5 mm and 1·7 mm, respectively. Recruitment of young adults, resulting in a decrease in the number of juveniles, was taken into account when calculating juvenile mortality. This population parameter was estimated on an annual basis from the total number of released mancae (N_{F}) and the number of next year's survivors, including juveniles as well as freshly maturated individuals:

$$M^{\mathrm{juv}} = \frac{N_{\mathrm{F}} - N_{t+1}^{\mathrm{juv}}}{N_{\mathrm{F}}} \qquad \text{eqn 3a}$$

and accordingly:

$$M^{\mathrm{ad}} = \frac{N_t - N_{t+1}^{\mathrm{ad}}}{N_t} \qquad \text{eqn 3b}$$

where N_{t+1}^{juv} and N_{t+1}^{ad} are the number of juveniles and adults, respectively, in N_{t+1}.

The annual change in population size, S, was calculated as

$$S = \frac{N_{t+1} - N_t}{N_t} \qquad \text{eqn 5}$$

STATISTICS

Data sets on mortality, reproduction and growth were not normally distributed. Consequently, results are presented as median ± median absolute deviation (M ± MAD; Sachs 1988). Prior to parametric statistics, data were transformed [$x' = \log(x + 1)$] to approximate normality and homoscedascity (cf. Levy 1980).

The effects of different food materials on juvenile growth and mortality were analysed using analyses of covariance (ANCOVA), with the experimentally manipulated pH level of the leaf litter serving as a covariate that had been used for changing microbial leaf litter colonization. Due to the data sets of two and three populations with four and three repeated observations, respectively, repeated measures ANCOVA was used. The 'leaf litter' (alder, birch or oak) and 'microbiota' (linear combination of the 'bacterial numbers' and microbial activity: 'low', 'medium', and 'high') served as factors.

For those population parameters that were significantly explained by the 'leaf litter' in ANCOVA, detailed effects of particular characteristics of the

leaf litter (cf. Table 1) were analysed with pH treatment and litter-colonizing microbiota (linear combination of microbial parameters) serving as covariates. Due to being in part causally related to each other, and to clustering different food varieties to classes of factors similarly, several leaf litter characteristics were combined to allow for definition of factors: 'toughness' (linear combination of physical strength, cellulose content and lignin content), 'softness' (*sensu* Zimmer & Topp 1997a: linear combination of water content and C:N ratio), and the content of phenolic compounds (phenolics, hydrolysable tannins, condensed tannins).

Results

Population densities of *P. scaber* (Figs 1 and 2) and *O. asellus* (Figs 3 and 4) oscillated due to reproduction and juvenile mortality, but also differed due to the effects of different food materials. Both the species and microbial conditioning of the leaf litter significantly affected reproduction and mortality of adults and thus changes in population size of *P. scaber* (Table 2a). The pH level of the leaf litter, serving as covariate, also significantly affected these population parameters, but not juvenile mortality that also could not be explained by the other factors of ANCOVA. Detailed analyses (ANCOVA) revealed that, besides pH and litter-colonizing microbiota (covariates: $P < 0{\cdot}001$), the 'softness' ($F = 222{\cdot}8$, $P < 0{\cdot}001$) and the content of phenolic compounds (phenolics: $F = 463{\cdot}9$, $P < 0{\cdot}001$; hydrolysable tannins: $F = 219{\cdot}7$, $P < 0{\cdot}001$; condensed tannins: $F = 47{\cdot}6$, $P < 0{\cdot}001$) of the leaf litter were significant for reproduction, but not its toughness ($F = 0{\cdot}3$, $P = 0{\cdot}613$). Similar results were obtained for changes in population size ('softness': $F = 11{\cdot}2$, $P = 0{\cdot}016$; phenolics: $F = 423{\cdot}3$, $P < 0{\cdot}001$; hydrolysable tannins: $F = 859{\cdot}6$, $P < 0{\cdot}001$; condensed tannins: $F = 149{\cdot}2$, $P < 0{\cdot}001$), but in this case, litter 'toughness' was significant, too ($F = 10{\cdot}1$, $P = 0{\cdot}019$). Adult mortality was also influenced by 'toughness' ($F = 57{\cdot}2$, $P < 0{\cdot}001$) and 'softness' ($F = 334{\cdot}3$, $P < 0{\cdot}001$), as well as phenolics ($F = 61{\cdot}3$, $P < 0{\cdot}001$) and hydrolysable tannins ($F = 499{\cdot}9$, $P < 0{\cdot}001$), but not by the content of condensed tannins ($F = 0{\cdot}4$, $P = 0{\cdot}567$).

Both reproduction and changes in population size showed within-factors variations that were significantly explained by the experimental date ('year' in Table 2b), but this effect was not significant for mortality of juveniles or adults.

P. scaber increased population size when fed with alder litter at pH 5·9 (cf. Figure 2a), while at other food materials populations declined due to lack in reproduction ('*qu3*'; Fig. 2b) or high mortality ('*al3*', '*be3*', '*be5*', '*qu5*'; Fig. 2c,d). When fed with birch litter at pH 3·3, the population went extinct after 3·5 years.

Population size in *O. asellus* was influenced by the leaf litter, but not by litter-colonizing microbiota (Table 3a). The same was also true for adult mortality and reproduction. By contrast, mortality of juvenile *O. asellus* depended on both physico-chemical characteristics and microbial colonization of the leaf litter. Adult and juvenile mortality were not correlated with the experimental pH treatment (covariate), although changes in population size and reproduction were; however, the latter was influenced neither by the leaf litter nor by litter-colonizing microbiota. This pattern was confirmed in detailed analyses (ANCOVA), when pH and litter-colonizing microbiota served as covariates. Adult mortality was influenced by the 'softness' of the leaf litter ($F = 34{\cdot}3$, $P = 0{\cdot}001$) and the content of tannins (hydrolysable: $F = 8{\cdot}9$, $P = 0{\cdot}016$; condensed: $F = 18{\cdot}6$, $P = 0{\cdot}005$), while in addition ('softness': $F = 329{\cdot}6$, $P < 0{\cdot}001$; hydrolysable tannins: $F = 58{\cdot}6$, $P < 0{\cdot}001$; condensed tannins: $F = 219{\cdot}7$, $P < 0{\cdot}001$) the content of phenolics ($F = 23{\cdot}9$, $P = 0{\cdot}001$) and litter-colonizing microbiota (covariate: $P = 0{\cdot}001$) were significant for juvenile mortality. The same was true for factors affecting changes in population size ('softness': $F = 278{\cdot}3$, $P < 0{\cdot}001$; phenolics: $F = 31{\cdot}3$, $P = 0{\cdot}001$; hydrolysable tannins: $F = 58{\cdot}6$, $P < 0{\cdot}001$; condensed tannins: $F = 110{\cdot}6$, $P < 0{\cdot}001$), while this population parameter correlated with the pH level (covariate: $P = 0{\cdot}008$), but not with litter-colonizing microbiota.

Both reproduction and changes in population size showed within-factors variations that were significantly explained by the experimental date ('year' in Table 3b), but this effect was not significant for mortality of juveniles or adults. Further, juvenile mortality was not influenced by the experimental covariate, pH level.

Alder litter resulted in increasing population size in *O. asellus* (cf. Fig. 4a). However, reproduction was about twice as high at pH 5·9 than at pH 3·5 (Fig. 4b), while adult and juvenile mortality was lower on alder litter at pH 3·5 than at pH 5·9 (Fig. 4c,d). Although reproduction was not significantly different when feeding on different leaf species at similar pH levels (cf. Fig. 3), high mortality on birch and on oak resulted in decreasing populations. Similarly to *P. scaber*, *O. asellus* reproduced more successfully on leaf litter at pH 5·5–5·9 than at pH 3·1–3·5. Populations of *O. asellus* went extinct when feeding on birch litter at pH 3·3.

Juveniles of *P. scaber* grew fast when fed with alder litter (Table 4), but significantly more slowly ($P < 0{\cdot}05$) when fed with birch or oak. Juvenile growth in *P. scaber* was affected by condensed tannins (ANCOVA: $F = 384{\cdot}2$, $P < 0{\cdot}001$) and by 'microbiota' ($F = 9{\cdot}1$, $P = 0{\cdot}009$), but not by the pH level of the litter (covariate).

Juveniles of *O. asellus* showed less marked differences in growth rates on different food materials

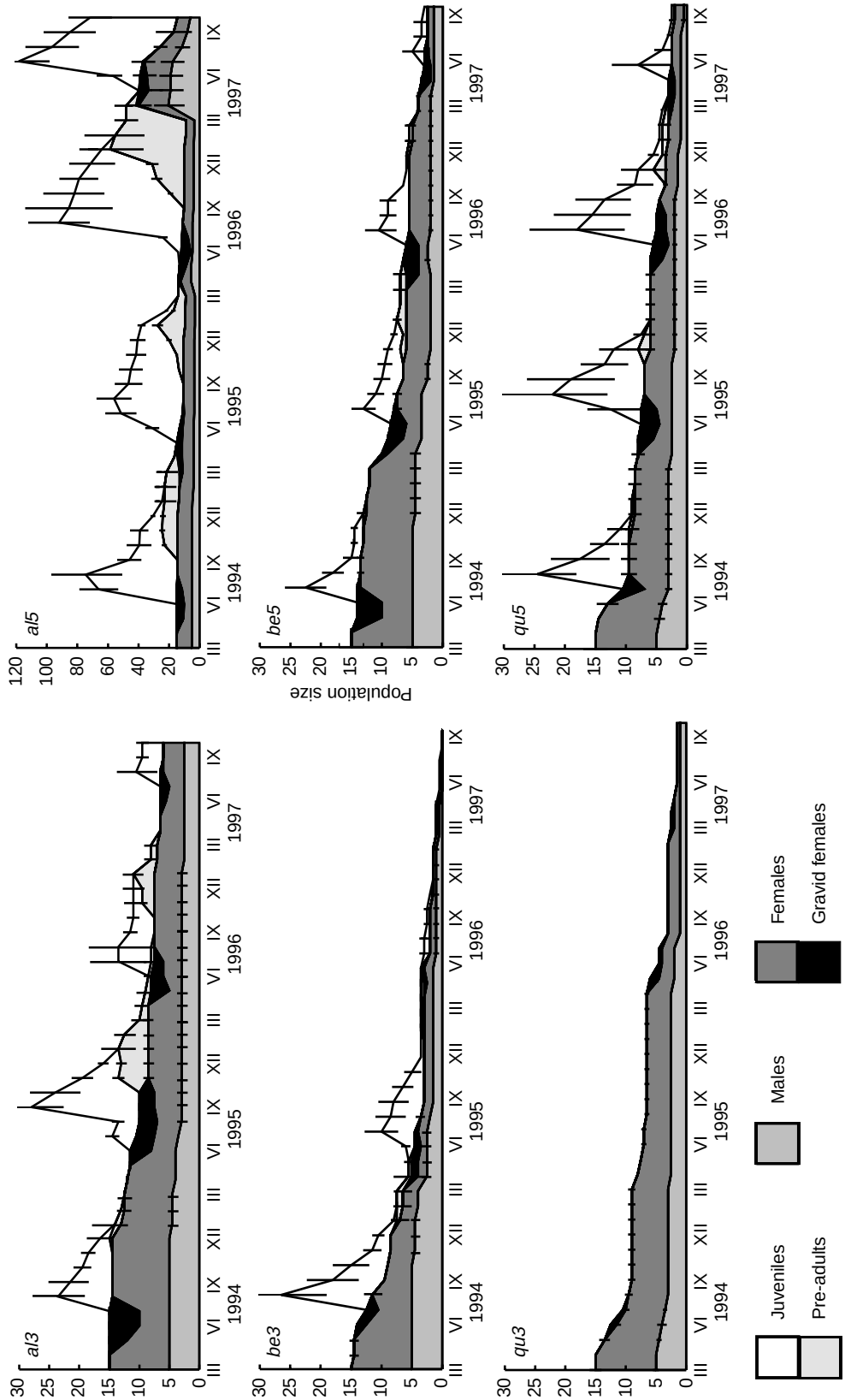

Fig. 1. Population dynamics of *Porcellio scaber* feeding on alder litter, pH 3·5 (*'al3'*) or pH 5·9 (*'al5'*), birch litter, pH 3·3 (*'be3'*) or pH 5·5 (*'be5'*), or oak litter, pH 3·1 (*'qu3'*) or pH 5·6 (*'qu5'*) in the laboratory from 1994 to 1997. Data are given as median and range of two populations of initially 15 adult isopods. Notice the different scaling in *'al5'*.

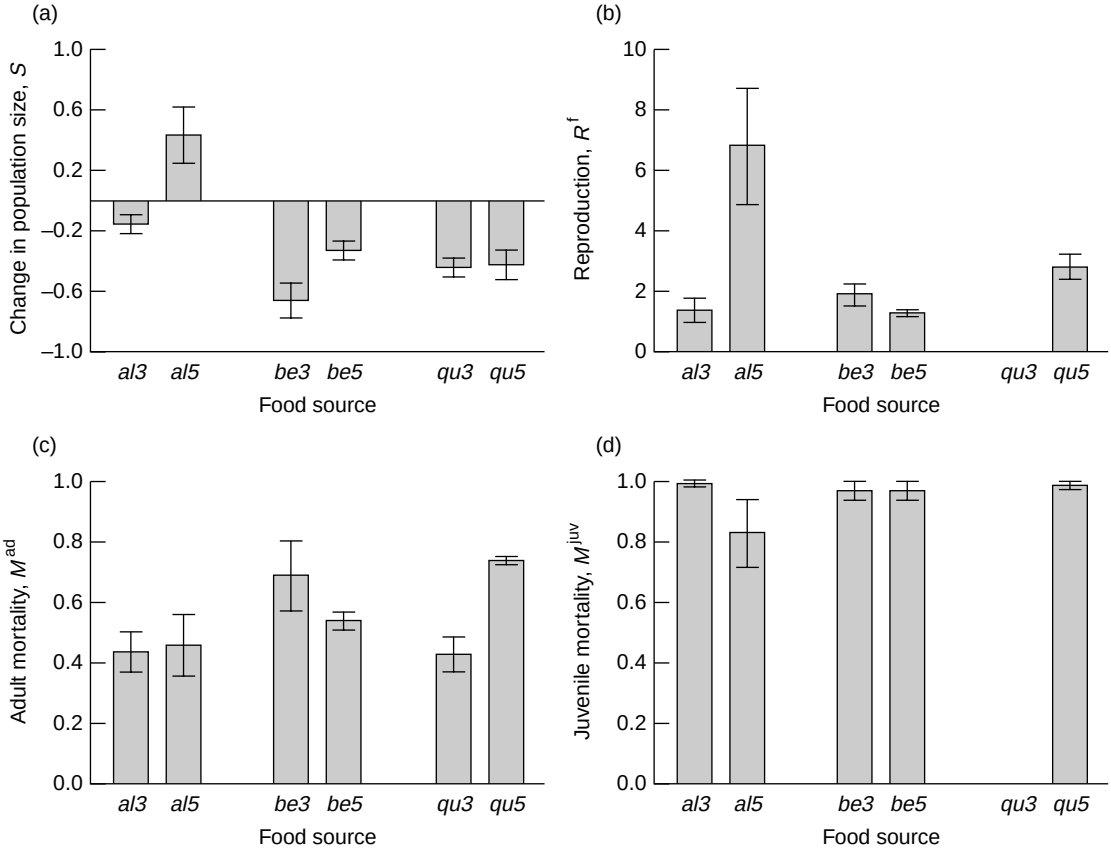

Fig. 2. Change in (a) population size, (b) reproduction, (c) adult mortality, and (d) juvenile mortality in populations of *Porcellio scaber* feeding on alder litter, pH 3·5 (‘*al3*’) or pH 5·9 (‘*al5*’), birch litter, pH 3·3 (‘*be3*’) or pH 5·5 (‘*be5*’), or oak litter, pH 3·1 (‘*qu3*’) or pH 5·6 (‘*qu5*’). Data are given as median ± median absolute deviation of repeated measures (4 years) for two populations (cf. Fig. 1).

(Table 5). On alder litter, young *O. asellus* grew slightly more slowly than on oak ($P < 0{\cdot}05$), birch litter resulting in intermediate values that did not differ from those obtained with the other species. In *O. asellus*, juvenile growth depended on the ‘toughness’ of the leaf litter (ANCOVA: $F = 284{\cdot}8$, $P < 0{\cdot}001$), but was independent of other leaf litter characteristics and ‘microbiota’ and ‘pH level’ (covariates).

Discussion

Numerous factors may help explain the coexistence of populations of sympatric woodlouse species and variations in population dynamics of these species. In previous studies on isopod populations, Brereton (1957), Sutton (1968, 1970) and Sunderland *et al.* (1976) described high juvenile mortality, resulting in seasonal oscillations of population size and structure

Table 2. Analyses of covariance (repeated measures) to estimate the effects of the species (‘leaf litter’) and the microbial colonization (‘microbiota’) of leaf litter, as influenced by pH treatment (covariate; between factors: a) and time (‘year’; within factors: b), on changes in population size (S), reproduction (R^f), and adult (M^{ad}) and juvenile mortality (M^{juv}), of *Porcellio scaber*

		S		R^f		M^{ad}		M^{juv}	
	d.f.	F	P	F	P	F	P	F	P
(a) pH treatment	1	801·9	0·001	664·3	0·001	67·5	0·001	1·8	0·237
Leaf litter	2	786·9	0·001	160·2	0·001	212·1	0·001	2·7	0·153
Microbiota	2	169·8	0·001	215·1	0·001	315·5	0·001	2·3	0·189
(b) Year	3	31·8	0·001	10·6	0·017	3·7	0·103	0·4	0·561
Year × pH treatment	3	6·9	0·039	13·6	0·011	1·4	0·276	0·5	0·522
Year × leaf litter	6	2·4	0·167	4·3	0·069	2·5	0·159	0.6	0·597
Year × microbiota	6	3·5	0·100	7·3	0·025	1·6	0·264	0·6	0·468

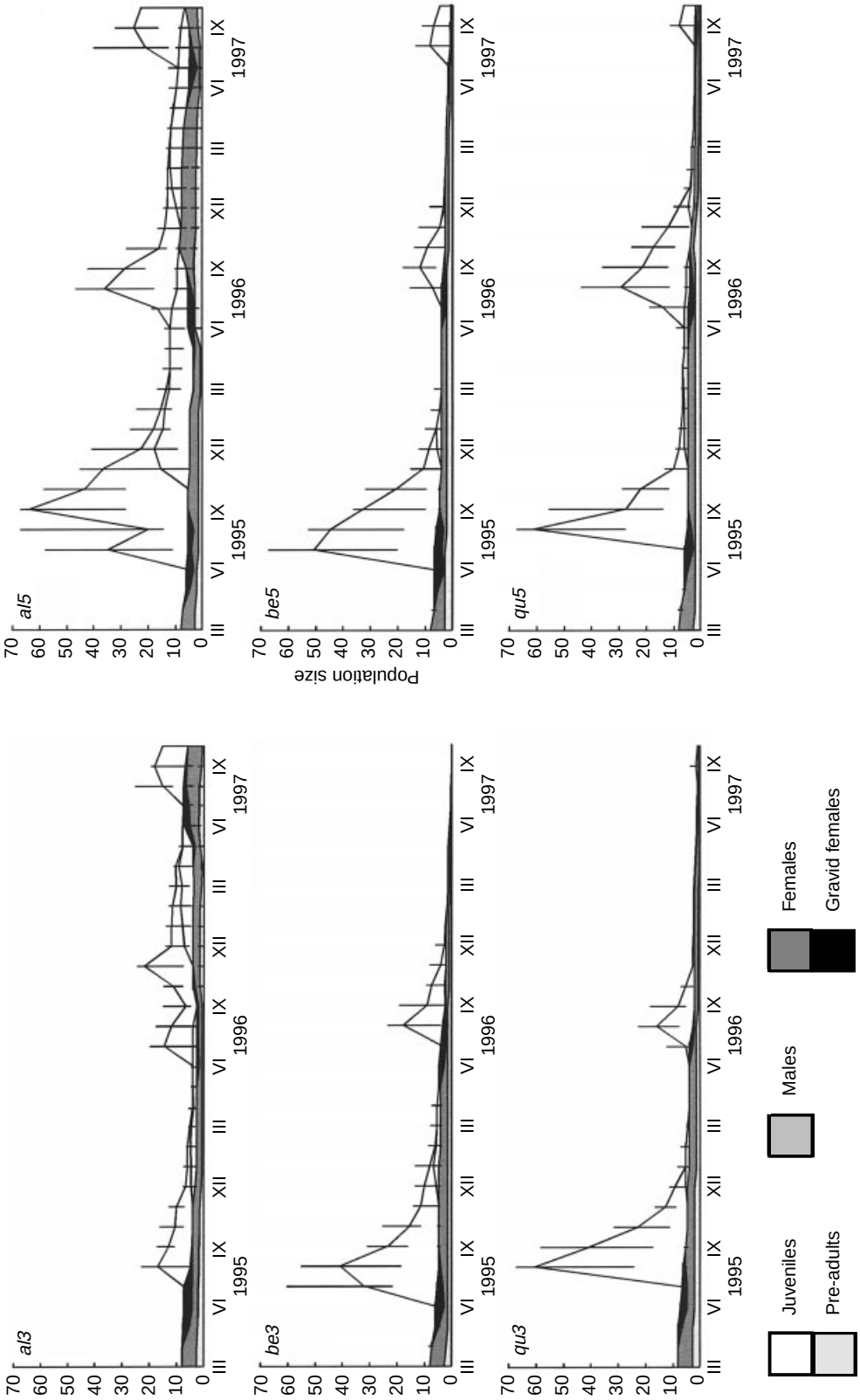

Fig. 3. Population dynamics of *Oniscus asellus* feeding on alder litter, pH 3·5 (*'al3'*) or pH 5·9 (*'al5'*), birch litter, pH 3·3 (*'be3'*) or pH 5·5 (*'be5'*), or oak litter, pH 3·1 (*'qu3'*) or pH 5·6 (*'qu5'*) in the laboratory from 1995 to 1997. Data are given as median and range for three populations of initially 8 adult isopods.

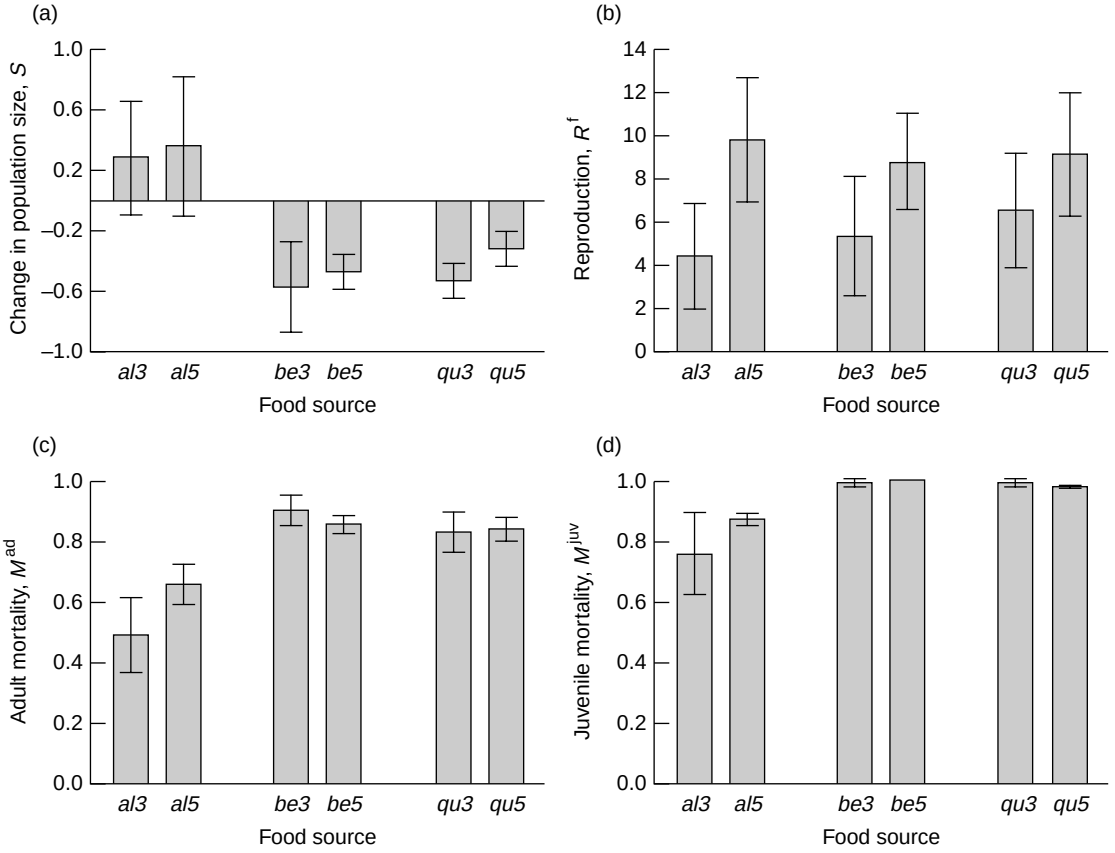

Fig. 4. Change in (a) population size, (b) reproduction, (c) adult mortality, and (d) juvenile mortality in populations of *Oniscus asellus* feeding on alder litter, pH 3·5 (‘*al3*’) or pH 5·9 (‘*al5*’), birch litter, pH 3·3 (‘*be3*’) or pH 5·5 (‘*be5*’), or oak litter, pH 3·1 (‘*qu3*’) or pH 5·6 (‘*qu5*’). Data are given as median ± median absolute deviation of repeated measures (3 years) for three populations (cf. Fig. 3).

(Miller & Cameron 1983; Warburg *et al*. 1984). Climatic variation has been shown to influence annual fluctuations of woodlouse populations (summarized in: Warburg *et al*. 1984). Results of the present study indicate that changes in population density may be driven by food quality (cf. Zimmer & Topp 1997a).

Phenolics are known to adversely affect the consumption of leaf litter by woodlice (Cameron & LaPoint 1978) and to increase mortality in *P. scaber* (Zimmer & Topp 1997a). The significance of phenolics and other chemical defences in plant tissue for its ingestion and digestion by animals was summarized by Rosenthal & Berenbaum (1992). By contrast,

Table 3. Analyses of covariance (repeated measures) to estimate the effects of the species (‘leaf litter’) and the microbial colonization (‘microbiota’) of leaf litter, as influenced by pH treatment (covariate; between factors: a) and time (‘year’; within factors: b), on changes in population size (S), reproduction (R^f), and adult (M^{ad}) and juvenile mortality (M^{juv}) of *Oniscus asellus*

		S		R^f		M^{ad}		M^{juv}	
	d.f.	F	P	F	P	F	P	F	P
(a) pH treatment (covariate)	1	26·2	0·002	44·9	0·001	0·1	0.822	165·4	0·148
Leaf litter	2	132·4	0·001	1·7	0·261	17·9	0·003	16·1	0·007
Microbiota	2	0·9	0·459	2·4	0·171	1·9	0·218	18·9	0·003
(b) Year	2	55·8	0·001	16·3	0·007	0·4	0·527	0·1	0·754
Year × pH treatment	2	31·3	0·001	2·1	0·206	0·1	0·726	0·1	0·845
Year × leaf litter	4	4·5	0·043	3·1	0·121	0·6	0·574	0·1	0·877
Year × microbiota	4	43·6	0·001	4·8	0·057	0·4	0·668	0·1	0·941

Table 4. Annual (1994–97) and overall (total) growth rates of juvenile *Porcellio scaber* feeding on different food materials. Growth rates (changes in head width, μm month^{-1}) are given as median ± median absolute deviation. *al3*, pH 3-manipulated alder litter; *al5*, pH 5-manipulated alder litter; *be3*, pH 3-manipulated birch litter; *al5*, pH 5-manipulated birch litter; *qu3*, pH 3-manipulated oak litter; *al5*, pH 5-manipulated oak litter

	1994/95	1995/96	1996/97	Total
al3	101 ± 11	106 ± 27	93 ± 27	100 ± 19
al5	101 ± 31	79 ± 22	121 ± 57	98 ± 41
be3	67 ± 31	56 ± 16	33 ± 32	56 ± 16
be5	83 ± 17	89 ± 16	87 ± 13	86 ± 16
qu3	No reproduction			
qu5	69 ± 33	98 ± 51	78 ± 16	80 ±16

nitrogen (White 1978; Topp 1981; Dunger 1983), or a low C:N ratio (Swift & Boddy 1984), positively affects consumption of saprophagous animals. White (1993) stated provocatively that a 'lack of access to nitrogen (...) is the major restriction on the abundance of animals'. Given that it is rather the availability of nitrogen than the total nitrogen content that is critical (White 1993), we would expect litter-colonizing microbiota, providing an easily accessible nitrogen source, to be of particular significance (cf. White 1993). Microbial activity of the leaf litter has been shown to increase food quality for *P. scaber* (Zimmer & Topp 1997a). Ingested microbiota are digested and utilized as food by both *O. asellus* (Gunnarsson & Tunlid 1986) and *P. scaber* (Zimmer & Topp 1998a), and support *P. scaber* in detoxifying hydrolysable tannins (Zimmer 1999a). Thus, we expected the density of litter-colonizing microbiota ('bacterial numbers' in Table 1) to affect the isopods' nutritional status, and consequently their longevity and reproduction. Further, enzymatic activity derived from ingested microbiota support digestive processes in isopods (e.g. Hassall & Jennings 1975; Kukor & Martin 1986). Thus, microbial activity (cf. Table 1) was expected to bias performance processes in isopods, too.

Table 5. Annual (1995–97) and overall (total) growth rates of juvenile *Oniscus asellus* feeding on different food materials. Growth rates (changes in head width, μm month^{-1}) are given as median ± median absolute deviation. For legend see Table 4

	1995/96	1996/97	Total
al3	89 ±16	67 ± 27	74 ± 41
al5	80 ± 15	67 ± 33	73 ± 40
be3	73 ± 25	99 ± 17	83 ± 32
be5	83 ± 17	97 ± 33	83 ± 37
qu3	92 ± 5	83 ± 37	89 ± 27
qu5	98 ± 33	83 ± 29	90 ± 34

P. scaber and O. asellus responded similarly to different leaf litter species in that adults of both species performed better on alder litter which had half the C:N ratio of the other species (ANCOVA: significant influence of 'softness'). Overall, adults of both species reproduced more offspring on litter varieties with high pH levels (pH 5·5–5·9) which may be due to either direct effects (ANCOVA: significant influence of the covariate) of low pH (3·1–3·5; cf. Zimmer & Topp 1997b) or to reduced contents of phenolic compounds (significant effects in ANCOVA) at higher pH (cf. Table 1). Thus, our results coincide with the predictions of White (1993) with respect to the limiting effect of nitrogen availability, as well as with the proposed significance of phenolic compounds (cf. Rosenthal & Berenbaum 1992).

Interspecific differences were observed with respect to the significance of litter-colonizing microbiota (linear combination of 'bacterial numbers' and microbial activity in our analyses). Litter-colonizing microbiota affected mortality and reproduction in adult *P. scaber*, but not in adult *O. asellus*. Similarly, juvenile growth rates depended on litter-colonizing microbiota in *P. scaber*, but not in *O. asellus*. Thus, our results confirm White's (1993) hypothesis with respect to the significance of microbiota serving as an easily available nitrogen source in *P. scaber*, but not in adult or juvenile *O.asellus*. Juveniles in particular would be expected to respond to differences in nitrogen availability (cf. White 1993).

Interspecific as well as intraspecific differences are further demonstrated by the comparison of adults and juveniles of *P. scaber* and *O. asellus*. Neither litter 'toughness' nor other food parameters could explain the variance in juvenile mortality in *P. scaber* (cf. Zimmer & Topp 1997a). The content of condensed tannins (but not 'toughness') and litter-colonizing microbiota influenced juvenile growth rates in this species. These results suggest that juvenile *P. scaber* forage by grazing on leaf litter rather than shredding it. In contrast, juveniles of *O. asellus* depended on most of the tested food parameters (including 'microbiota') with respect to mortality, but only on 'toughness' with respect to growth. Thus, juvenile *O. asellus* may differ from juvenile *P. scaber* by shredding leaf litter rather than grazing. Further, the opposite significance for litter 'toughness' and microbiota were observed in adults of both species, compared with the respective juveniles, suggesting the avoidance of intraspecific competition between adults and juveniles.

Interspecific differences between adults with respect to the significance of litter 'toughness' may reflect differences either in mouth part morphology (cf. Hassall 1977) or in the capability of digesting the corresponding leaf litter compounds. Detailed comparative studies on morphology and enzymatic

equipment are required to further understand this aspect of sympatry in woodlice.

In conclusion, the present study suggests interspecific differences between *O. asellus* and *P. scaber* in the utilization of food, as has been deduced previously from the results of a field study (Zimmer & Topp 1999). For saprophagous soil animals, the access to food of high quality is limited (Rushton & Hassall 1983b; White 1993). Given that food quality is largely determined by the microbial colonization for *P. scaber* (Zimmer & Topp 1997a; this study), while *O. asellus* predominantly depends on physicochemical characteristics of the leaf litter (this study), competition of these sympatric species for food appears to be partly avoided, allowing for their sympatric coexistence.

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