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Leaf litter-colonizing microbiota: supplementary food source or indicator of food quality for *Porcellio scaber* (Isopoda: Oniscidea)?

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Abstract

Different explanations have been proposed for why terrestrial isopods prefer, and gain from, feeding on microbially inoculated food materials. In the present study, no-choice feeding experiments are used to test three contrasting, but not mutually exclusive, hypotheses. (1) The digestion and nutritional utilization of microbial cells enhance the nutritive value of leaf litter; (2) extracellular digestive enzymes of microbial origin promote digestion of leaf litter; (3) leaf litter-colonizing microbiota serve as indicators for easily digestible leaf litter of high nutritive value. Predictions derived from these hypotheses are compared with the results of a study with experimentally manipulated leaf litter, serving as food sources for the common woodlouse *Porcellio scaber*. Leaf litter-colonizing microbiota increased consumption of leaf litter by isopods and contributed somewhat to biomass gain of isopods, but not to the assimilation of ingested food. Thus, the present results coincide with predictions derived from hypothesis (3) suggesting that leaf litter-colonizing microbiota stimulate consumption by indicating high food quality. Their positive effects on assimilation and growth, however, are context-specific, being stronger in case of high-quality food than in case of low-quality food.

Keywords: Digestion; Leaf litter-colonizing microbiota; Microbial activity; Nutrition; Terrestrial isopods

1. Introduction

Isopods (Isopoda: Oniscidea) enhance the decomposition rate of leaf litter directly and indirectly [10,12,14]. Direct contributions include the comminution of leaf litter [6,9,10,12,18] and the digestive degradation of cellulose [9,41] and phenolic leaf litter compounds [19,34,42]. Indirect contributions include the ingestion of saprotrophic leaf litter-colonizing microbiota and egestion of their propagules in surface-increased substrate (feces), thus enhancing microbial activity [6,18,28].

On the other hand, isopods gain from feeding on microbially inoculated leaf litter [29,39], and population dynamics of isopods are positively influenced by feeding on leaf litter with high microbial activity and/or biomass [14,39,43]. Due to the digestion of ingested microbiota [8,22,41], microbial biomass may significantly contribute to nutrition by providing essential nutrients [4,5,30], or ingested microbiota may assist in pH homeostasis [40]. Further, microbial extracellular enzymes that have been ingested along with microbially inoculated leaf litter are utilized for digestive processes [11,17,34]. In this context, microbial processing of leaf litter prior to ingestion has to be considered, too; isopods preferentially consume decaying leaf litter [9,12,22] that is characterized by reduced toughness [22] and low contents of phenolics and other deterrent compounds [16,21,35].

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Based on this, two hypotheses explaining the preference of isopods for microbially inoculated leaf litter arise: (1) the digestion and nutritional utilization of microbial cells enhance the nutritive value of leaf litter; (2) extracellular digestive enzymes of microbial origin promote digestion of leaf litter during the gut passage. Digestion and nutritional utilization of microbiota (*hypothesis 1*) as well as utilizing microbial digestive enzymes (*hypothesis 2*) would be expected to result in increased digestibility of the food and enhanced mass gain of isopods. However, the role of ingested microbiota and their enzymatic activity in cellulose degradation [11,17] in the isopod gut has recently been debated (see [36]). Besides being a supplementary food source or a source of digestive enzymes, leaf litter-colonizing microbiota may also serve as phagostimulating indicators for easily digestible leaf litter of high nutritional value exhibiting low contents of recalcitrant or deterrent compounds (*hypothesis 3*): Indeed, previous studies [38] proved foraging *Porcellio scaber* Latr. to respond positively to air-borne metabolites of leaf litter-colonizing microbiota, indicating olfactory perception of these compounds. If in addition gustatory perception of microbiota through contact-chemoreception stimulated feeding, microbial colonization of leaf litter would be expected to increase consumption, whereas digestive processes and growth might be promoted only marginally.

The present study was performed to test the above contrasting, but not mutually exclusive, hypotheses that explain why terrestrial isopods gain from feeding on microbially inoculated food materials. Predictions derived from these hypotheses are compared with the results of a study using experimentally manipulated leaf litter as food sources for *Porcellio scaber*, that differed with respect to microbial activity and biomass, and exhibited different leaf litter characteristics due to microbial processing.

2. Materials and methods

2.1. Animals

Isopods (*Porcellio scaber* Latr. 1804) were collected in the vicinity of Cologne, Germany. Prior to the experiments, they were collectively maintained at 15 °C (16 h light, 8 h dark) in translucent plastic boxes the bottoms of which were covered with moist plaster of Paris, and fed mixed deciduous leaf litter.

During the experiments, isopods (N = 24 per treatment) were kept individually in Petri dishes, containing only the food source (either about 40 mg (dry mass) oak litter or about 50 mg (dry mass) alder litter; see below) and a moist piece of terra cotta for maintaining humidity. Each Petri dish containing a single isopod served as a single unit of replication. Petri dishes were stored in plastic boxes, the bottoms of which were covered with moist filter paper, at 15 °C, 16 h light, 8 h dark.

Only pre-adult individuals with a live mass of 10–20 mg (3–6 mg dry mass) were used for feeding trials, to obtain high consumption and growth rates [32], and were assigned to different food sources randomly. The experiments lasted 14 days, making the gravimetrical detection of mass changes possible (accuracy of ±0.1 mg), but reducing the probability of molting events (every 3–5 weeks) that would have affected consumption and mass gain. To compensate for oscillations in live mass due to changes in body water content, isopods were weighed daily, and changes in live mass during the experiment were obtained through linear regression analyses of live mass vs. time. By this technique, we did not obtain significant deviations from the linear model, and average mass gain could be calculated as the difference between the calculated (linear regression) body mass at the start and the end of the experiment. Dry mass was calculated using a live mass–dry mass regression (N = 15).

2.2. Food sources

Leaf litter of oak (*Quercus robur* L.) and alder (*Alnus glutinosa* (L.) Gaertn.) was collected in the vicinity of Cologne (Germany) immediately after leaves had been shed, and microbial activity was reduced by air-drying [39] prior to storage in the laboratory. Air-dried leaf litter was either re-wetted immediately before being offered as food with low microbial activity, or was microbially inoculated in a pool of freshly collected leaf litter for 21 days at 20 °C [39] before being offered as food with high microbial activity. In the present study, air-dried and re-wetted leaf litter exhibited significantly lower microbial density and activity than leaf litter after experimental microbial inoculation (Table 1). Further, microbial inoculation resulted in significantly reduced leaf litter strength, phenolic contents, and C:N ratios as compared with air-dried and re-wetted litter types (Table 1). This side-effect of experimental inoculation, due to microbial leaf litter processing, was aimed here to take into account the quality-increasing effects of microbial processing.

Besides using air-dried and re-wetted (henceforth: "air-dried") vs. inoculated leaf litter, we further experimentally manipulated microbial and physico-chemical characteristics of the leaf litter (cf. [39,43]) by soaking the litter in solutions of sulphurous acid, pH 2, pH 4, or pH 6, for 7 days and subsequent air-drying prior to microbial inoculation or re-wetting [39]. Besides changing the composition of microbial communities [1], acidification affects both microbial biomass [1,2,14,15] and activity [14,15,39,40]. Thus, manipulation of leaf litter at different pH levels results in substrates that differ in suitability for microbial colonization, with an optimal pH of about 5.0 [39,40,43]. In the present study, both cellulase activity (determined after [24]), providing a measure of one of the most important functional groups of leaf litter-colonizing microbiota (cf. [24]), and microbial density significantly dropped in response to litter acidification (Table 1).

Food sources were characterized in terms of pH value (3 M KCl), water content (gravimetrically), phenol content (Folin-Ciocalteu assay, as described in [33]), and the C:N

Table 1
Characteristics of leaf litter serving as experimental food sources of *Porcellio scaber*, as influenced by the tree species, pH manipulation, and microbial inoculation. Data are presented as median ± median absolute deviation (N = 24)

		Alnus glutinosa						*Quercus robur*					
pH manipulation		2.0	4.0	6.0	2.0	4.0	6.0	2.0	4.0	6.0	2.0	4.0	6.0
Microbial inoculation		No	No	No	Yes	Yes	Yes	No	No	No	Yes	Yes	Yes
pH level		2.9 ± 0.1	4.6 ± 0.1	5.5 ± 0.1	3.0 ± 0.1	4.2 ± 0.1	5.5 ± 0.1	2.6 ± 0.1	4.5 ± 0.1	6.5 ± 0.1	3.1 ± 0.1	5.0 ± 0.1	6.3 ± 0.1
Cellulolytic activity [a]	µg Glc(g h)$^{-1}$	3.7 ± 1.7	7.7 ± 0.8	11 ± 1	9.1 ± 0.8	44 ± 5	58 ± 3	2.2 ± 0.3	2.6 ± 0.9	3.1 ± 0.2	10 ± 0.4	32 ± 1	26 ± 1
Microbial density [b]	10^{10} cells g^{-1}	0.3 ± 0.1	0.6 ± 0.2	0.9 ± 0.3	3.5 ± 0.1	4.3 ± 0.5	4.6 ± 0.6	0.2 ± 0.1	0.4 ± 0.2	0.4 ± 0.1	1.9 ± 0.7	3.2 ± 0.7	4.2 ± 0.9
Water content [c]	%	70 ± 3	74 ± 2	80 ± 2	34 ± 4	43 ± 5	47 ± 3	73 ± 2	72 ± 3	73 ± 4	61 ± 3	49 ± 2	62 ± 2
Physical strength [d]	g mm^{-2}	22 ± 7	46 ± 4	24 ± 6	13 ± 2	14 ± 5	12 ± 2	65 ± 6	89 ± 10	73 ± 8	58 ± 5	39 ± 5	41 ± 8
Phenolics [e]	mg g^{-1}	24 ± 1	23 ± 1	14 ± 1	29 ± 2	7.8 ± 0.3	4.2 ± 0.1	24 ± 1	43 ± 3	19 ± 1	4.5 ± 0.1	4.1 ± 0.2	3.7 ± 0.1
C:N ratio [f]		20 ± 1	20 ± 1	24 ± 1	15 ± 1	16 ± 1	16 ± 1	38 ± 1	35 ± 1	30 ± 1	30 ± 1	28 ± 1	29 ± 1

[a] As described in [25].
[b] Acridine orange-staining.
[c] Gravimetrically.
[d] Modified after Tanton (1962) [27].
[e] As described in [33].
[f] N: Kjeldahl method; C: total organic carbon analyzer.

ratio (N: Kjeldahl method; C: Total Organic Carbon analyzer, Ströhlein, Kaarst, Germany). Although it has been suggested to use more than one measure to accurately describe microbial activity [24], mainly enzymatic activity of leaf litter-colonizing microbiota with the potential to aid in digestion of leaf litter were of interest. Thus, solely cellulolytic activity was determined according to [24]. As an estimate of microbial density, cells were counted under an epifluorescence microscope after staining with acridine orange. Differences between the 12 food sources, as they occurred after the experimental treatment, are indicated in Table 1. For the sake of clarity, the entity of changes resulting from pH manipulation are henceforth summarized by mentioning the respective pH treatment; distinguishing between air-dried and inoculated leaf litter henceforth includes the corresponding changes in leaf litter characteristics. By contrast, "pH level" describes the actual pH of manipulated leaf litter as offered as food in the experiments (cf. Table 1).

A total of 12 different litter materials were offered as food in no-choice feeding experiments. Each food source was offered in amounts that were expected to be consumed by about 80% by the end of the feeding experiment [24]. Thus, each Petri dish contained either ca. 40 mg dry mass oak litter or ca. 50 mg dry mass alder litter (as estimated from the results of pre-experiments). Besides delivering optimal accuracy of consumption data [23], these food amounts prevented physiological adaptations to food shortage [13]. Initial dry mass of food sources was estimated through wet mass:dry mass ratios (60 °C, 24 h; $N = 15$). During feeding experiments, feces were removed daily to reduce coprophagy and to allow for the quantitative determination of feces dry mass ($N = 24$).

2.3. Isopod performance

From the data on mass change in isopods, the data for dry mass loss of the food, and the dry mass of daily collected feces, *consumption* ((mg food ingested)/(day × g animal)), *assimilation* (% mass loss of ingested food due to digestion: 100 × (mg food ingested – mg food egested)/(mg ingested food)), and *growth* ((mg dry mass change)/(day × g animals)) were calculated.

In order to test isopods for direct response to chemical differences between freshly fallen and microbially processed leaf litter, preferences tests based on contact-chemoreception of water-soluble leaf litter compounds were performed using "arched globes" (after [37]), made of 12 filter paper arches that can be soaked with test solutions. Each filter paper arch (length 25 mm; width: 5 mm) joining two other arches in an angle of 120° at each of its tips, respectively, these arches form a globe of approximately 50 mm in diameter. The size of the arches is chosen as to serve as an inverse treadmill for an isopod that has been fixed at a boom through an adhesive tape. In this experimental design, an isopod will have to decide where to go (left or right) whenever it reaches an arch-joint. If the two alternative arches differ with respect to the soaked food extract, we obtain information of multiple two-way-choices [31]. Here, the filter paper arches were soaked with aqueous extracts of either freshly fallen or microbially processed litter.

2.4. Statistics

Most of the present data were not normally distributed. Consequently, data are presented as median, quartiles and range (minimum–maximum), and predominantly non-parametric statistics were used for comparison of data sets. Multivariate comparison was performed with Kruskal–Wallis H tests. Subsequently, significant differences were localized by using Bonferroni-corrected Mann–Whitney U tests.

For further statistical analysis, an ANCOVA approach was chosen, because the litter pH, serving as covariate here, is known to directly affect isopod nutrition (e.g. [39]), but was simply used as means to experimentally change leaf litter characteristics in the present study (see above). Prior to these parametric statistics, data were transformed to normality and approximate homoscedasticity [18]. The two measures for microbial density and biomass used in the present study were significantly correlated with each other (Spearman correlation of mean values: $P < 0.001$, $N = 12$). Thus, these parameters were combined by means of linear combination (cf. [39]), and the resulting data were converted into factorial levels.

Preference tests were analyzed using resampling statistics (poptools: http://www.csiro.au/vbc/poptools) with 9999 iterations, according to [3].

3. Results

As illustrated in Fig. 1A, consumption of oak litter depended on the experimental pH manipulation and the resulting changes in leaf litter characteristics (cf. Table 1). Highest consumption was obtained when isopods were fed pH 4-manipulated leaf litter. Microbial inoculation increased consumption of leaf litter ($P < 0.05$) in every pH treatment in similar ways; comparing microbially inoculated materials, pH 4-manipulated leaf litter was consumed most extensively, while isopods ingested least of pH 6-manipulated oak litter, with pH 2-manipulated leaf litter revealing intermediate values. When isopods were fed air-dried alder litter (Fig. 1B), pH 2-manipulated leaf litter (pH 2.9) was consumed in smaller amounts ($P < 0.05$) than that with higher pH. Microbial inoculation led to higher consumption rates ($P < 0.01$) in case of pH 2- and pH 6-manipulation, but had little effect of consumption with pH 4-manipulated litter.

Assimilation of oak litter (Fig. 2A) was highest when isopods were fed microbially inoculated pH 4-manipulated leaf litter, but did not differ between the other treatments. By contrast, assimilation efficiencies were highest when *P. scaber* fed pH 2-manipulated alder litter (Fig. 2B). Alder litter with higher pH levels resulted in lower assimilation efficiencies of 27% and 22% ($P < 0.05$) that did not differ

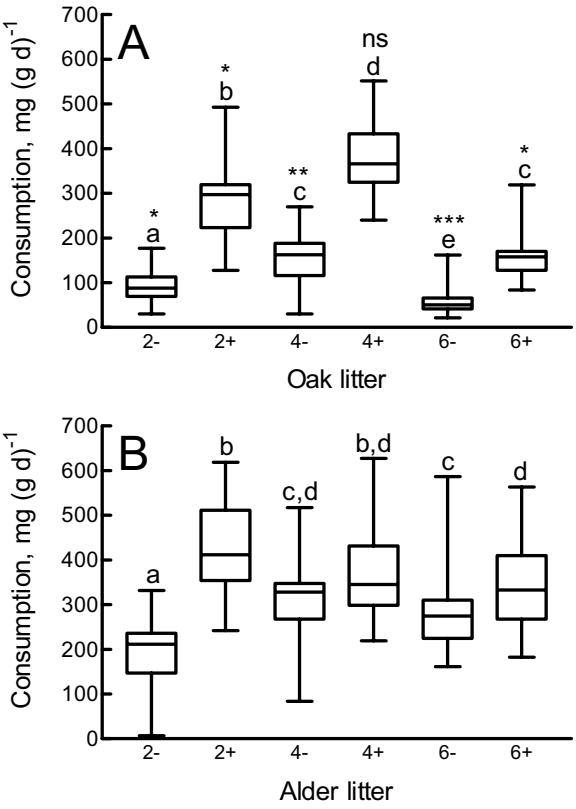

Fig. 1. Consumption of different food sources derived from oak (A) or alder (B) by *Porcellio scaber*—2: pH 2-manipulated; 4: pH 4-manipulated; 6: pH 6-manipulated; –: air-dried and re-wetted; +: microbially inoculated. Box plots represent the range (minimum–maximum), the first and third quartile, and the median (N = 24). Different lower-case letters indicate significant differences (α = 0.05) among different food sources derived from oak (A) or those derived from alder (B). Asterisks in (A) indicate differences between food source treatments derived from oak and alder (Bonferroni-corrected U tests; ns: not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

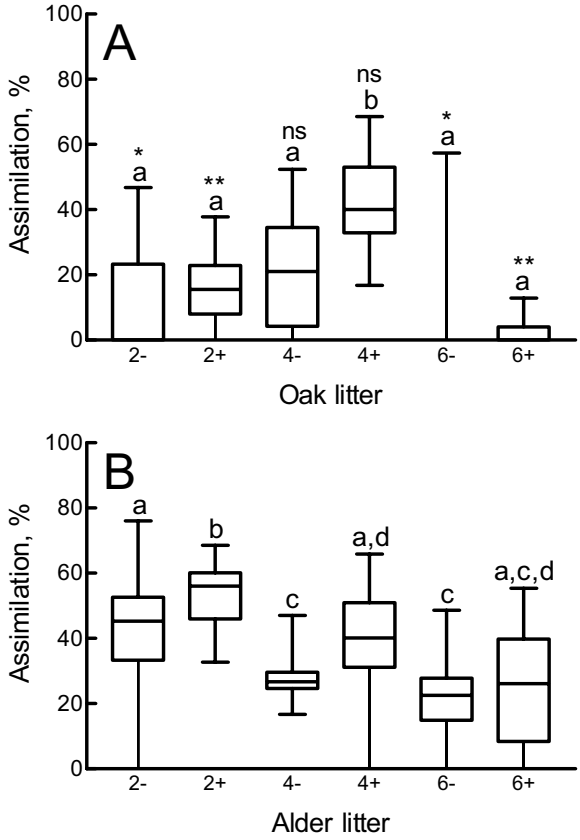

Fig. 2. Assimilation of different food sources derived from oak (A) or alder (B) by *Porcellio scaber*—for further explanation see legend to Fig. 1.

from each other ($P > 0.8$). Microbial inoculation of alder litter increased assimilation as long as pH was below 5 (pH 2- and pH 4-manipulated), but overall led to similar assimilation efficiencies as air-dried leaf litter, when comparing different pH treatments.

Porcellio scaber gained little biomass from feeding on air-dried oak litter (Fig. 3A), and pH treatments did not differ from each other ($P > 0.4$). Microbial inoculation did not result in higher growth rates when fed pH 2- or pH 6-manipulated oak litter ($P > 0.7$), but inoculated oak litter with pH 5.0 (pH 4-manipulated) resulted in biomass loss in most isopods. Air-dried alder litter with pH levels above 3 (pH 4- and pH 6-manipulated), however, allowed for biomass gain (Fig. 3B), while alder litter with pH 2.9 (pH 2-manipulated), on average, resulted in unchanged biomass after 14 days. Only for this experimental manipulation did microbial inoculation increase growth rates ($P < 0.05$). Growth rates did not differ between pH treatments ($P > 0.6$).

ANCOVA (Table 2) indicated an influence of the "leaf litter" and its microbial activity and density ("microbiota") on consumption. Similar effects of leaf litter characteristics were evident for the assimilation of ingested food, but in this case, "microbiota" were insignificant. The variance in growth of *P. scaber* was explained by an interaction of "leaf litter" and "microbiota" (Table 2), indicating that the effect of the former depended on the latter and vice versa.

In preference tests, isopods distinguished between extracts of oak and alder litter by contact chemoreception, preferring the latter one if the leaf litter had been microbially processed ($P < 0.05$; N = 657 decision by nine isopods). By contrast, extracts of freshly fallen oak and alder litter was not distinguished ($P > 0.6$; N = 502 decisions by nine isopods).

4. Discussion

Isopods exhibit a strong preference for microbially colonized leaf litter [7,26,27] to which they seem to be attracted by air-borne microbial metabolites [38]. *Hypothesis 1* concerns the nutritive gain from ingesting microbially colonized

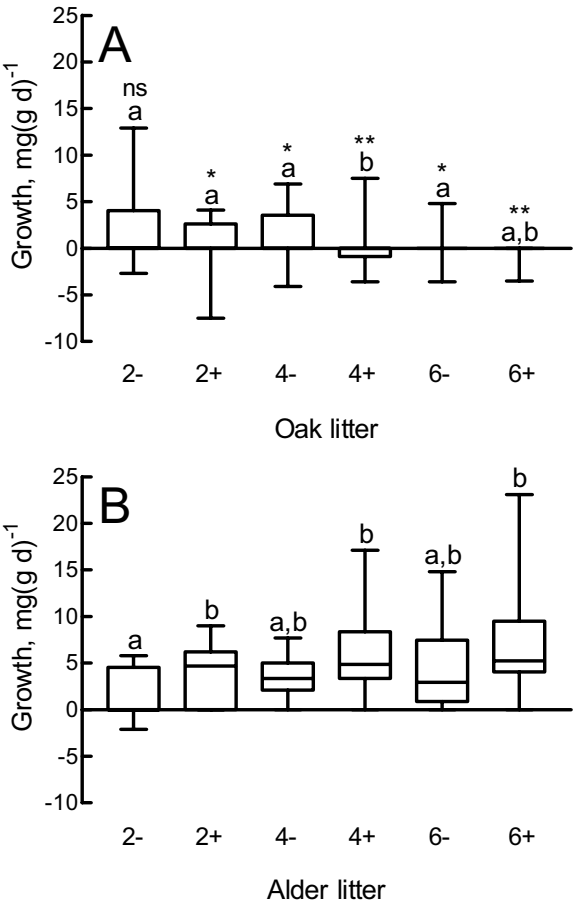

Fig. 3. Growth of *Porcellio scaber* feeding upon different food sources derived from oak (A) or alder (B)—for further explanation see legend to Fig. 1.

food sources due to microbial biomass providing an easily accessible source of nutrients [8,21,30], whereas *hypothesis 2* is related to microbial enzymes being active in the hindgut lumen and supporting digestive processes [11,17,34]. On the other hand, the olfactory orientation of foraging isopods towards sites of microbial activity [38] may simply reflect the isopods' utilization of dense microbial populations and high microbial activity as an indicator for an easily digestible food source (*hypothesis 3*) that is low in recalcitrant and deterrent compounds. This may even be due to different microbial species colonizing different litter types (M. Mews and M. Zimmer, unpublished), and thus, indicating different food sources.

Microbial processing of leaf litter prior to ingestion by isopods enhances leaf litter palatability [9,12,22] and quality [29,30,39,43] by, e.g., reducing the C:N ratio and/or the content of phenolic compounds [16,20,34,35]. Thus, the indication of easily digestible leaf litter may partially be due to its microbial processing. To that extent, it is difficult to distinguish experimentally between microbial processing vs. microbial enzymes being active inside the hindgut in terms of increased digestibility, but the results of the present preference tests provide evidence for direct gustatory perception (without the possibility of digestive feedback) of either microbial biomass or degradation products due to microbial activity. Since isopods did not differentiate by taste between litter types of low vs. high quality (i.e., oak vs. alder; cf. Figs. 2 and 3) in case of freshly fallen litter but did so after microbial processing, leaf litter-colonizing microbiota and/or the products of their activity appear to indicate high-quality food.

When *P. scaber* was fed leaf litter, microbiota (as well as the litter type) influenced consumption (*hypothesis 3*), but, in contrast to predictions derived from *hypotheses 1* and *2*, isopods did not gain mass from ingesting microbial biomass (measured by means of cell density here) nor did they benefit from microbial cellulases or processing prior to ingestion in terms of increased assimilation efficiency. Thus, leaf litter-colonizing microbiota provide phagostimulating indicators for easily digestible leaf litter of high nutritional value (*hypothesis 3*) rather than microbial biomass (*hypothesis 1*) or enzymatic activity (*hypothesis 2*). Doubtlessly, however, microbiota are digested [8,21,41] and may serve as a source of essential nutrients [4,5,30], microbial enzymes are active during the gut passage [11,17], and microbial processing of leaf litter increases its digestibility [22,29,40].

This study is the first to directly compare predictions derived from different hypotheses on why isopods gain from feeding on microbially inoculated leaf litter with experimental data. From the present results, it is obvious that there is no simple answer to the question of whether leaf litter-colonizing microbiota mainly provide nutrients or enzymes

Table 2
Analyses of covariance (ANCOVA), explaining the variance in consumption and assimilation by, and growth of, *Porcellio scaber* fed on different leaf litter materials. Covariate: manipulated pH level; factors: leaf litter species ("leaf litter", cf. Table 1), microbial activity and density ("microbiota", cf. Table 1)

ANCOVA	df	Consumption		Assimilation		Growth	
		F	*P*	*F*	*P*	*F*	*P*
Model	5	247.1	<0.001	42.8	<0.001	26.6	<0.001
Covariate	1	0.8	0.376	6.3	0.013	1.1	0.291
Leaf litter	1	64.7	<0.001	23.5	<0.001	31.5	<0.001
Microbiota	1	74.4	<0.001	1.1	0.318	5.8	0.001
interactions Leaf litter × microbiota	1	1.1	0.286	0.8	0.359	9.8	<0.001

to litter-feeding isopods. Previous findings [41,42] hint at the limited significance of leaf litter-colonizing microbiota with respect to the origin of digestive enzymes in *P. scaber*. By reducing the number of endosymbiotic bacteria in midgut glands, Zimmer and Topp obtained reduced activity of cellulose degrading [41] and phenol oxidizing [42] enzymes, while no such effect resulted from reduced numbers of ingested hindgut microbiota [34]. Thus, bacterial endosymbionts, rather than ingested leaf litter-colonizing microbiota, were proposed to contribute to the digestion of recalcitrant leaf litter compounds. On the other hand, early studies clearly indicated the involvement of ingested microbial enzymes in leaf litter digestion [11,17]. The present results, obtained from feeding experiments with experimentally manipulated leaf litter, do not support this point of view, nor do they present evidence for microbiota serving as a supplementary food source.

The tree species from which the leaf litter derived, was the only factor to affect all the tested parameters of nutrition in *P. scaber* (Table 2). However, statistical interactions between this factor and "microbiota" indicate that microbial inoculation alters the effect of leaf litter characteristics on growth. This may be due to readily available microbial nutrients that are ingested along with inoculated leaf litter (*hypothesis 1*) or to ingested microbiota providing enzymes that facilitate leaf litter digestion (*hypothesis 2*), and thus, utilization of ingested nutrients. Further, different litter types contain different microbial communities (M. Mews and M. Zimmer, unpublished); thus, microbial inoculation and processing can be expected to affect the nutritive quality of different litter types in different ways. Apparently, leaf litter-colonizing microbiota supported growth on food of already high quality (e.g., alder) in the present study, whereas no such effect occurred in case of litter of low nutritive value (e.g., oak). Since microbiota affected growth but not leaf litter assimilation, an involvement of easily accessible microbial nutrients rather than of microbial digestive enzymes is probable. Further, given that food sources that get readily colonized by microbiota are also easily digestible to isopods, leaf litter-colonizing microbiota evidently serve as an indicator of high-quality food, and microbial metabolites promote feeding.

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