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Consumption Performance of Five Detritivore Species Feeding on *Alnus glutinosa* L. Leaf Litter in a Microcosm Experiment

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Abstract: The present study was performed to assess the feeding performance of five detritivore species in a microcosm design. The test animals were four millipede species, *Telodeinopus aoutii* (Demange), *Epibolus pulchripes* (Gerstäcker), *Cylindroiulus caeruleocinctus* (Wood), *Glomeris hexasticha* (Brandt), and one isopod species, *Porcellio scaber* (Latreille), all feeding on *Alnus glutinosa* L. leaf litter for five consecutive weeks. At the end of each one-week interval, litter consumption, animal fresh weight, and excrement production were measured. Then, the feeding activity parameters for each species were calculated. Between big-size animal species, higher leaf consumption rates of 12.3–30.9 mg dry weight day^{-1} individual^{-1} were calculated for *T. aoutii* compared to those of 3.72–8.25 mg dry weight day^{-1} individual^{-1} for *E. pulchripes*. However, there was no difference in the consumption rates among small-size animals ranging from 0.46 to 1.65 mg dry weight day^{-1} individual^{-1}. Excrement production rates followed a similar trend, as the consumption rates and the animals' body weight remained constant during the experiment. Time was an important factor influencing the feeding activity of the animals, especially for the big-size group. Overall, the average assimilation efficiency of these species varied from 13.7% to 53.3%. The results of the present work will be the first step for understanding the ecological needs of these decomposer species in soil ecosystems.

Keywords: assimilation efficiency; degradation processes; feeding activity; litter decomposition; millipedes; organic matter; soil detritivore

1. Introduction

Decomposition of organic matter is an important stage in soil formation and its developmental process and soil functions [1,2]. Soil detritivore species are involved in the fragmentation of dead plant materials, their incorporation into soil, and mixing them with the mineral particles [3–5]. Moreover, during litter decomposition, inorganic nutrients are released to the surrounding environment [6,7]. In this way, detritivore species may contribute to the nutrient cycling and availability of these nutrients to other soil organisms. Leaf litter deposition into the soil and its transformation to organic matter and nutrients may improve soil quality. In the organic-matter developmental process, both soil invertebrates and microorganisms have important roles. Microbial communities also help enhance decomposition of leaf litter by their specific enzymes. Moreover, soil invertebrate may facilitate microbial colonization due to the fragmentation of leaf litter and increasing its surface area [8–10]. Therefore, their interaction is very important for plant material decomposition [11].

Energy budget experiments are one of the methods to investigate the feeding behavior and activity of soil organisms contributing to leaf litter decomposition. In these tests, we would be able to calculate the energetic parameters of the organisms, such as leaf litter consumption rate, animal production (growth) rate, and excrement production rate, to get more information about the ecophysiological mechanisms attributed to the soil functions and their processes. These parameters show how the organisms divide their energetic costs, which are taken from their food for their maintenance, survival, growth, and reproduction [12]. In some studies, the energy-budget modeling approach has been used to provide a comprehensive framework for mathematically investigating animal physiology, life history, and population dynamics (e.g., [13,14]). Using energy budget experiments will help researchers find out more about the essential requirements of the organisms for having maximum trade-off between their energy investments in their natural habitats.

Among soil invertebrates, millipedes and isopods are two main groups widely found in natural ecosystems and have great influence on organic matter decomposition [15]. They can break down organic matter and are involved in soil developmental processes [16–18]. Investigating their feeding activities and food consumption will shed more light on their role in decomposition of leaf litter in soil [19,20]. In the present study, we used a few millipede species and one isopod species, to further assess their consumption performance when feeding on the alder plant litter *Alnus glutinosa*.

There are studies in the literature in which the feeding activities of soil organisms have been studied (e.g., [20–22]). However, information on the ecophysiological aspects of millipede and isopod species' feeding behavior with emphasize on their energetics is not well documented. Therefore, the aim of the present study was to investigate the feeding performance of millipede and isopod species, considering their feeding activity parameters attributed to leaf consumption in a pot experiment. We hypothesized that different energetic parameters could be obtained for different species, and test animals may show different feeding activities when they consume alder leaf litter at different time intervals.

2. Materials and Methods

2.1. Test Plant

The alder species *A. glutinosa* leaf litter was used for comparing animal consumption in the present study. The selected alder species is one of the most widespread broad-leaf tree species the forests, as it can be found in most of Europe, Southwest Asia, and Northern Africa. Freshly fallen plant leaves were collected from a forest close to České Budějovice, Czech Republic. Leaf litter was first air-dried in lab condition and then dried in an oven at 60 °C, for 24 h, to have the dry weight of leaves at the beginning of each interval.

2.2. Animals

Five test species were used in our experiment, including four millipede species, *Telodeinopus aoutii* (Kenyan millipede; Diplopoda: Spirostreptida), *Epibolus pulchripes* (red-legged millipede; Diplopoda: Spirobolida), *Cylindroiulus caeruleocinctus* (Diplopoda: Julida), and *Glomeris hexasticha* (pill millipede; Diplopoda: Glomerida), and one isopod/woodlouse species, *Porcellio scaber* (Isopoda: Oniscidea, Porcellionidae) (Figure S1). These millipedes and isopod species are common, ecologically relevant species which have been used in previous ecophysiological studies. All animal species have been cultured in our lab for several years. The first two big-size species (*T. aoutii* and *E. pulchripes*) were kept at 25 °C and relative humidity of 60%, similar to their natural tropical habitats. However, the last three small-size species were kept at 15 °C, since these species are mostly found in European conditions. They fed with leaf litter or wood pieces in the main cultures. At the start of the experiment, individuals were selected from the main stock, starved for 2 days, and distributed in the experimental containers (8.5 × 9 × 4.5 cm). These plastic boxes were aerated through holes in the lid.

2.3. Experimental Design

In each experimental container, 1.0–2.0 g oven-dried leaf litter of *A. glutinosa* was added at the beginning of each interval for the big-size animals. For the small-size animals, this was 0.5–0.6 g. The amount of leaf litter for each animal species was determined based on pilot tests (Ardestani, unpublished). The dry leaves were sprayed with distilled water only at the beginning of the test. The experimental containers were kept in a big box containing water, in order to moisturize the atmosphere of the box. This allowed the leaves to be moistened and palatable for the animals during each interval. Suitability of this method was proved before in the pilot tests. Five individuals from each species were added to the plastic containers. The produced excrements were collected every day from each replicate and stored in separate containers, to prevent microbial activity. Four replicates were considered for all test species.

The experiment was conducted for five consecutive intervals, with the same condition, and with each of them lasting for one week. As control, four replicate experimental containers were kept at the same experimental conditions as for the animal species (at 25 and 15 °C). To these containers, 0.4–0.5 g dry weight of leaf litter was added, and their final dry weight was measured at the end of each interval, to account for microbial activities (degradation).

2.4. Plant Litter, Animal Weight, and Excrement

The remaining leaf litter at the end of each interval was collected, oven-dried at 60 °C for 24 h, and weighed as unconsumed dry weight of leaves. Litter consumption (g) for each animal species was calculated from the difference between the unconsumed dry weight and the initial dry weight (see full method in Supplementary Materials). At the end of each interval, the animals from each replicate were weighed as the end-fresh weight. The daily collected excrements from each replicate were compiled at the end of each interval and weighed (fresh and dry weight after oven-drying at 60°C for 24 h).

At the beginning of the test, two animals were taken directly from the main culture, and their fresh and dry weight (after freezing and drying at 60 °C for 24 h) was obtained. The same was done with the two animals randomly taken from the experimental containers at the end of the test, to account for the end-animal measurements. The fresh and dry weights of these sampled animals were also used for the calculation of feeding-activity parameters (see Supplementary Materials). All dry materials were weighed by using a micro balance (KERN, EG 620-3NM, Balingen, Germany; measuring biomass weight to 0.001 g, with high accuracy).

2.5. Data Analysis

For comparing the difference in the consumed leaf litter, fresh weight of animals, and excrements produced among different animal species at different intervals, two-way analysis of variance (ANOVA) was used. Litter consumption and excrement production among intervals were compared with one-way ANOVA for each animal species separately. The detailed method for calculating feeding activity parameters is shown in Supplementary Materials. Statistica 13.3 program package (www.tibco.com/products/tibco-statistica) was used for statistical analyses.

3. Results

Consumption of *A. glutinosa* leaf litter was significantly affected by animal species ($F_{4,75} = 445$, $p < 0.001$), intervals ($F_{4,75} = 21.3$, $p < 0.001$), and the interaction of animal species x time ($F_{16,75} = 10.6$, $p < 0.001$). Higher leaf consumption was observed in the big-size animals (*T. aoutii* and *E. pulchripes*; Figure 1a) compared to the small-size animals (*C. caeruleocinctus*, *G. hexastica*, and *P. scaber*). However, litter consumption was significantly decreased till the end of experiment for *T. aoutii* (Figure S2a, Supplementary Materials; $F_{4,15} = 17.4$, $p < 0.001$), *C. caeruleocinctus* ($F_{4,15} = 3.66$, $p < 0.05$), and *P. scaber* ($F_{4,15} = 4.93$, $p < 0.01$), but not for *E. pulchripes* ($F_{4,15} = 2.75$, $p = 0.07$) and *G. hexastica* ($F_{4,15} = 2.54$, $p = 0.08$). In the last two species, only a slight decrease in their leaf litter feeding was observed in the first interval, and then it remained constant in the other intervals (Figure S2a).

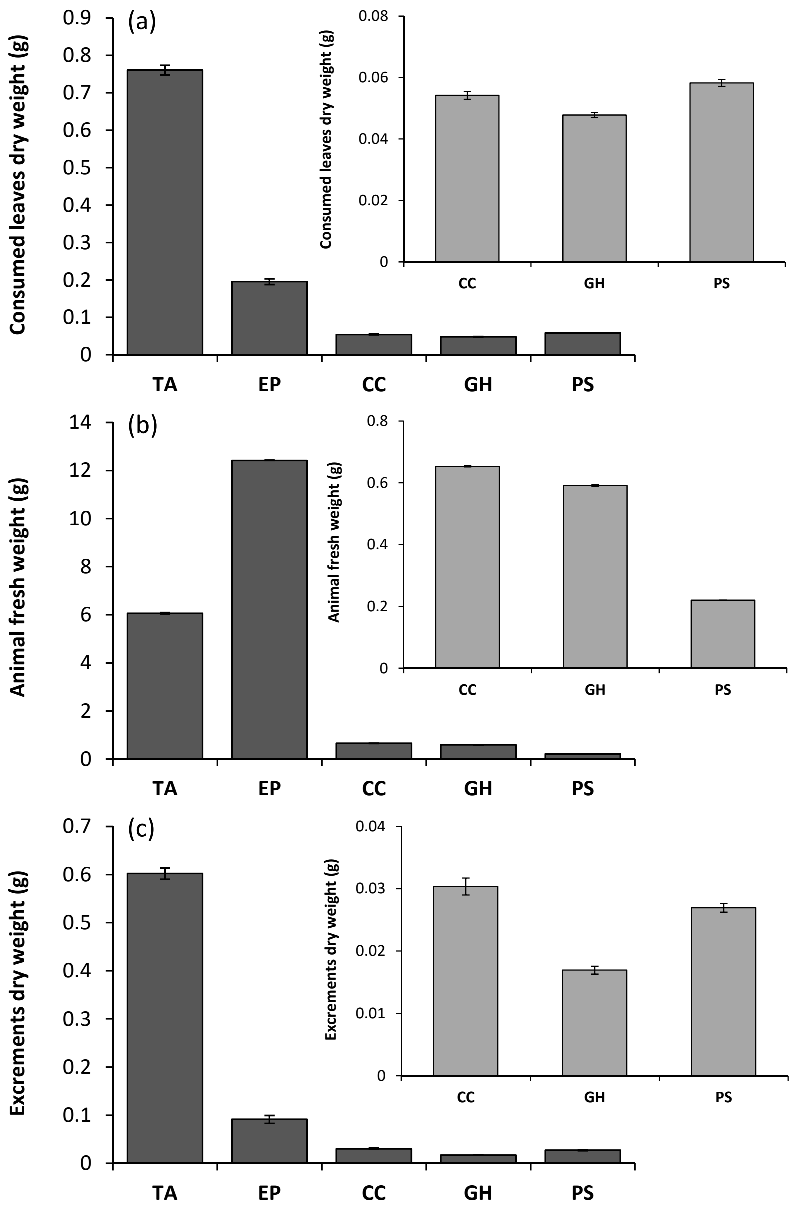

Figure 1. The consumed leaf litter (**a**), animals' fresh weight (**b**) and produced excrements (**c**) for five detritivore species feeding on *Alnus glutinosa* in a five-interval test. The animal species were *Telodeinopus aoutii* (TA), *Epibolus pulchripes* (EP), *Cylindroiulus caeruleocinctus* (CC), *Glomeris hexasticha* (GH), and *Porcellio scaber* (PS). The two big-size species (*T. aoutii* and *E. pulchripes*) were kept at 25 °C, similar to their natural tropical habitats, and the three small-size species were kept at 15 °C. The duration of each interval was one week. Four replicates for each interval/animal were used. The columns are the average of five intervals ± standard error (SE). All values are based on total dry weight (g) measured at the end of each interval.

Produced excrements were significantly influenced by animal species (Figure 1c and Figure S2c; $F_{4,75} = 374$, $p < 0.001$), intervals ($F_{4,75} = 20.3$, $p < 0.001$), and the interaction of animal species x time ($F_{16,75} = 9.90$, $p < 0.001$). Excrement production was significantly decreased till the end of experiment for *T. aoutii* (Figure S2c; $F_{4,15} = 16.5$, $p < 0.001$), *E. pulchripes* ($F_{4,15} = 4.22$, $p < 0.05$), and *P. scaber* ($F_{4,15} = 3.07$, $p = 0.05$), but not for *C. caeruleocinctus* ($F_{4,15} = 1.77$, $p = 0.19$) and *G. hexastica* ($F_{4,15} = 2.04$, $p = 0.14$).

Calculated feeding activity parameters showed that litter consumption rate was highest for *T. aoutii* among other test species (Table 1). The values of 12.3–30.9 mg dry weight day^{-1} individual^{-1} for *T. aoutii*, 3.72–8.25 mg dry weight day^{-1} individual^{-1} for *E. pulchripes*, 0.47–1.53 mg dry weight day^{-1}

individual^{-1} for *C. caeruleocinctus*, 0.46–1.32 mg dry weight day^{-1} individual^{-1} for *G. hexastica*, and 0.61–1.65 mg dry weight day^{-1} individual^{-1} for *P. scaber* were obtained. Leaf consumption rates decreased in all species from the first interval to the fifth interval (Table 1). When comparing the values based on the initial fresh body weight of the animals (g), litter consumption rates were independent of animal size. Highest litter consumption rates belonged to *P. scaber*, ranging from 14.3 to 39.4 mg dry weight day^{-1} $g_{fresh\ body\ weight}^{-1}$ (Table S1, Supplementary Materials). For *T. aoutii*, *E. pulchripes*, *C. caeruleocinctus*, and *G. hexastica*, these values were 10.3–21.8, 1.54–3.18, 3.14–11.8, and 3.81–10.9 mg dry weight day^{-1} $g_{fresh\ body\ weight}^{-1}$, respectively. Excrement production rates of 10.1–25.3 mg dry weight day^{-1} individual^{-1} for *T. aoutii* were higher compared to those of 1.28–6.60 mg dry weight day^{-1} individual^{-1} for *E. pulchripes*, 0.67–1.13 mg dry weight day^{-1} individual^{-1} for *C. caeruleocinctus*, 0.26–0.71 mg dry weight day^{-1} individual^{-1} for *G. hexastica*, and 0.48–1.04 mg dry weight day^{-1} individual^{-1} for *P. scaber* (Table 1). Moreover, almost all animal production rates (growth) were zero, due to the slight changes in the animals' body weight during the experiment (see also Table S2, Supplementary Materials).

Assimilation rates of 2.17–5.54 mg dry weight day^{-1} individual^{-1} for *T. aoutii*, 1.65–3.07 mg dry weight day^{-1} individual^{-1} for *E. pulchripes*, 0.02–0.40 mg dry weight day^{-1} individual^{-1} for *C. caeruleocinctus*, 0.19–0.61 mg dry weight day^{-1} individual^{-1} for *G. hexastica*, and 0.03–0.61 mg dry weight day^{-1} individual^{-1} for *P. scaber* were calculated. Assimilation efficiency in the animal species ranged between 17.4% and 24.2% for *T. aoutii* (with the average of 19.3%), 20.0% and 70.6% for *E. pulchripes* (with the average of 53.3%), 3.19% and 26.2% (with the average of 13.7%) for *C. caeruleocinctus*, 26.7% and 55.2% (with the average of 40.5%) for *G. hexastica*, and between 4.93% and 48.1% (with the average of 29.2%) for *P. scaber* at different intervals. Generally, a slight increase in assimilation efficiency of test species could be found even when the leaf consumption rates decreased in different test species during the experiment (Figure 2). Production efficiency values were all close to zero, since the animals' body weight remained constant during the experiment (Table 1 and Figure S2b).

Table 1. The consumption rate, animal growth rate, and excrement production rate (mg dry weight day^{-1} individual^{-1}) for five detritivore species feeding on *Alnus glutinosa* leaf litter in a five-interval test. The animal species were *Telodeinopus aoutii*, *Epibolus pulchripes*, *Cylindroiulus caeruleocinctus*, *Glomeris hexasticha*, and *Porcellio scaber*. The first two, the big-size species (*T. aoutii* and *E. pulchripes*), were kept at 25 °C, similar to their natural tropical habitats, and the last three, the small-size species, were kept at 15 °C. The duration of each interval was one week. Four replicates for each interval/animal were used. The feeding activity parameters were calculated based on the method described in Supplementary Materials.

Animal species	Time	*Telodeinopus aoutii*	*Epibolus pulchripes*	*Cylindroiulus caeruleocinctus*	*Glomeris hexasticha*	*Porcellio scaber*
Litter consumption rate	Interval 1	30.9	8.25	1.50	1.32	1.34
	Interval 2	25.6	4.14	1.53	0.46	1.65
	Interval 3	19.3	4.34	0.72	0.70	1.05
	Interval 4	18.2	4.68	0.78	0.83	0.92
	Interval 5	12.3	3.72	0.47	0.78	0.61
Animal growth rate	Interval 1	0.00	0.00	0.00	0.00	0.02
	Interval 2	0.00	0.00	0.00	0.00	0.00
	Interval 3	0.06	0.00	0.00	0.06	0.01
	Interval 4	0.00	0.79	0.18	0.07	0.03
	Interval 5	0.00	0.31	0.00	0.04	0.00
Excrement production rate	Interval 1	25.3	6.60	1.13	0.71	0.99
	Interval 2	21.1	2.01	1.13	0.26	1.04
	Interval 3	15.6	1.28	0.69	0.31	0.76
	Interval 4	13.8	1.68	0.67	0.56	0.48
	Interval 5	10.1	1.48	0.71	0.57	0.58

4. Discussion

The results of the present study showed that our test species had different consumption patterns when feeding on *A. glutinosa* (Figure 1). The consumption performance can be compared within two groups: big-size and small-size species. In the big-size group, *A. glutinosa* was more palatable for *T. aoutii* than for *E. pulchripes*, even with higher initial fresh weight of the latter test species. This suggests a negative correlation between leaf consumption and body mass, which may be attributed to the leaf litter chemical characteristics, such as C and N content, lignin, polyphenol, and condensed tannin contents (e.g., [20]). Previous studies supported this assumption that leaf litter consumption and its decomposition positively correlated with leaf N content in different soil organisms [23–25]. In the small-size group, *A. glutinosa* showed similar palatability for all animals (Figure 1). Palatability of leaf litter for these species might depend on several factors, such as litter nutritive value, toughness, and levels of feeding deterrents [15,26]. Quadros et al. [27] reported that *A. glutinosa* was more attractive than *Acer pseudoplatanus*, *Betula pendula*, *Fagus sylvatica*, and *Quercus robur* leaf litter for *P. scaber*.

Our results showed a decrease in leaf consumption of big-size test species (Figure S2a) over time. However, for *E. pulchripes*, the animals could keep their feeding activity constant after the first interval. Moreover, this trend was observed for *C. caeruleocinctus* and *P. scaber* in the small-size group. One of the reasons for decreasing leaf consumption, especially in big-size animals, is their diverse food resources and different feeding activities in their natural environment. Here, we have only provided one litter species, which could be less attractive to them. However, they kept feeding during the test, and their body weight did not change up to the fifth interval (Figure S2b). This may also indicate that large part of the acquired energy went into maintenance, not into growth. They exhibited reduced consumption but still kept feeding in larger amounts (also see below); for example, such behavior was observed in *T. aoutii* (Figures 1 and S2) when forced to feed on alder leaf litter with high N content under our laboratory conditions. The C/N ratio of 14.6 was measured for *A. glutinosa* [28].

Leaf consumption rates of 0.46 to 30.9 mg dry weight day^{-1} individual^{-1} calculated for the millipede species in the present study (Table 1) are in agreement with the values of 5–35 mg dry weight day^{-1} individual^{-1} reported for the millipede *G. marginata* fed on two grass species, *Bromus erectus* and *Festuca rubra* [29]. Our values for *G. hexastica* were ten times lower than the values of 5.72–14.1 mg dry weight day^{-1} individual^{-1} reported for leaf consumption of this species feeding on oak, maple, and beech leaf litter [30]. This indicates that *G. hexastica* did not show much interest in eating Alnus leaf litter compared to those mentioned litter species. David and Gillon [31] also reported the values up to 51 mg dry weight mg$_{\text{fresh weight}}^{-1}$ day^{-1} for *G. marginata* feeding on holm oak (*Q. ilex*) leaf litter. Latter values based on fresh body weight of animals are also higher than those of 3.81–10.9 for *G. hexastica* in our study (Table S1), but plant species and animal species (*marginata* vs. *hexastica*) are different.

Moreover, litter consumption rates of 0.61–1.65 mg dry weight day^{-1} individual^{-1} obtained for the isopod *P. scaber* are much lower than the values of 20–30 mg dry weight day^{-1} individual^{-1} for the isopod *Armadillidium vulgare* [32]. Consumption rates of 0.34 and 0.70 mg dry weight mg$_{\text{fresh body weight}}^{-1}$ day^{-1} were reported for two isopod species, *Balloniscus glaber* and *Atlantoscia floridana*, respectively, when feeding on mixed leaf litter in Southern Brazil [33]. These values, however, are much lower than our results for *P. scaber* (Table S1). This suggests the species-specific difference for their feeding activities. David et al. [32] showed that leaf litter type and duration of the test had significant effects on leaf litter consumption rates by the isopod species *A. vulgare*. For example, consumption rates up to 60 mg dry weight day^{-1} individual^{-1} were obtained for *Medicago minima* after 12 days of test, but the values were much lower (up to 5 mg dry weight day^{-1} individual^{-1}) for *Trifolium angustifolium* and *Lolium rigidum*. The latter values are in agreement with the obtained values for *P. scaber* in the present study. This again emphasizes that the leaf consumption rate for each animal group is species-specific and completely dependent on the test plant and animal species. This also indicates that the litter quality (e.g., N content) could be an important factor for observing different consumption performance of these detritivore species.

Among millipede species, the assimilation efficiency of 26.7%–55.2% for *G. hexastica* obtained in the present study is similar to the value of 29% measured for *G. marginata* fed with freshly fallen *Q. ilex* leaf litter under Mediterranean conditions simulated in the laboratory [31]. The values of 20.4% to 43.6% for assimilation efficiency of *G. hexastica* were obtained when feeding on oak, maple, and beech leaf litter [30], and these values are consistent with our values. Calculated assimilation efficiency of 4.93% to 48.1% for *P. scaber* in the present study is in agreement with the values of 50.3% to 67.8% reported for this species when feeding on beech leaves and spruce branchlets [34]. Assimilation efficiency of 27% and 31% was reported for two isopod species, *B. glaber* and *A. floridana*, respectively, when feeding on mixed leaf litter in Southern Brazil [33]. It should be noted that assimilation efficiency may have a negative relationship with the size of animals, especially when comparing two millipede species (big-size vs. small-size), *T. aoutii* and *G. hexastica*. The reason for that is not clear, but a decrease in leaf litter consumption under this laboratory condition could be one of the main reasons. This microcosm system may be too artificial for the animals to resemble their natural habitat. Each species has special mechanisms and strategies to cope with their food ingestion since they are feeding with a single food source here.

Our results showed that assimilation efficiency in our test species generally increased even when litter consumption was decreased (Figure 2). This is consistent with few other studies in which inverse relationship between assimilation efficiency and the ingestion rate were reported [35–37]. This suggests that even animals that consume a lower amount of food assimilate it more efficiently. By this way, they are able to keep the energetic needs of their body in a balanced state. Different mechanisms for increasing assimilation efficiency with decreasing leaf consumption can be considered. One of them could be related to the difference in enzymatic capabilities of these detritivore species. For example, Beck and Friebe [38] found that gut extracts of the millipede *Polydesmus angustus* were more active against polysaccharides than those of the woodlouse *Oniscus asellus*. Another reason for increasing assimilation efficiency could be related to the fact that leaf litter may have already infected with microbial communities, thus increasing its digestibility (e.g., [39,40]). This may increase their efficiency in food utilization, since microorganisms use special enzymes (i.e., cellulolytic) to ingest leaf materials [41]. This has been confirmed by the latter author in terrestrial isopods to be dependent on microbial colonization.

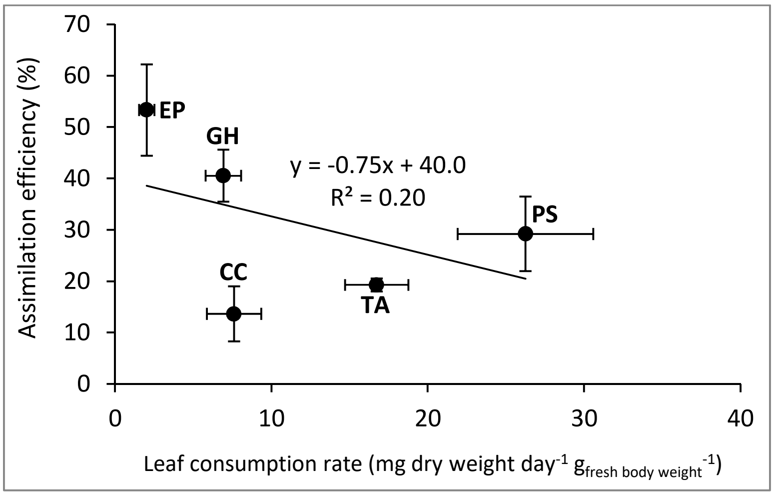

Figure 2. The relationship between assimilation efficiency and leaf litter consumption rates for five detritivore species feeding on *Alnus glutinosa*. The animal species were *Telodeinopus aoutii* (TA), *Epibolus pulchripes* (EP), *Cylindroiulus caeruleocinctus* (CC), *Glomeris hexasticha* (GH), and *Porcellio scaber* (PS). The experiment was performed for five consecutive weeks, with each interval lasting one week. Four replicates for each interval/animal were used. The assimilation efficiencies are in percentage, and the leaf litter consumption rates are in mg dry weight day^{-1} $g_{fresh\ body\ weight}^{-1}$. Data points represent the average values ± standard error (SE) for all test species and for all intervals.

5. Conclusions

The results of the present study showed that leaf consumption and excrement production rates are species-specific when four detritivore millipedes and one isopod species fed on *A. glutinosa* leaf litter. Time was an important factor affecting the consumption performance of all test species, especially big-size millipedes. Their litter consumption decreased till the end of experiment. Assimilation efficiency was also dependent on the test species and varied between 13.7% and 53.3%. Similar feeding activity parameters were obtained for our test species compared to the literature. The impact of macroarthropods on litter decomposition may have potentially important implications in the functioning of forest ecosystems, which are characterized by energy and nutrient flows, cycling, biomass production, and decomposition of organic matter. Since these test species are mixed-litter decomposers in natural environment, more research is needed for investigating their feeding activities, using different leaf litter types and analyzing their quality, in simulated experimental conditions.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1. Figure S1: The animal species used in the feeding experiment: *Telodeinopus aoutii* (TA), *Epibolus pulchripes* (EP), *Cylindroiulus caeruleocinctus* (CC), *Glomeris hexasticha* (GH), and *Porcellio scaber* (PS). Figure S2: The consumed leaf litter (a), animals' fresh weight (b), and produced excrements (c) for five detritivore species feeding on *Alnus glutinosa* in a five-interval test. Table S1: The consumption rate, animal growth rate, excrement production rate, and assimilation rate (mg dry weight day^{-1} $g_{fresh\ body\ weight}^{-1}$) for five detritivore species feeding on *Alnus glutinosa* leaf litter in a five-interval test. Table S2: The calorimetric values for five detritivore species feeding on *Alnus glutinosa* leaf litter in a five-interval test.

Author Contributions: J.F. and V.S. conceived of and designed the experiments; M.M.A. performed the experiments. M.M.A. and V.S. analyzed the data; M.M.A. wrote the manuscript; and other authors provided editorial advice.

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Conflicts of Interest: The authors declare that there are no conflicts of interest.

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