

Leaf litter ingestion and assimilation by two endemic pill millipedes (*Arthrosphaera*)

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Abstract This study aims to determine leaf litter preference, consumption rate, growth rate, food conversion efficiency, and quality of fecal pellets of two endemic pill millipedes (*Arthrosphaera dalyi* and *Arthrosphaera davisoni*) of the Western Ghats of India by laboratory microcosm experiments. Among seven combinations of three plantation leaf litters offered in 4-day trial, top three preferred combinations were selected for 4-week trial. In 4-week trial, preference of mixed litter diet was higher than single litter diet, which resulted in enhanced growth as well as food conversion efficiency of millipedes. Among *Hopea*, *Pongamia*, and *Areca* litters, *A. dalyi* preferred *Hopea*+*Pongamia*, and its consumption was significantly correlated with contents of organic carbon ($P<0.05$; $r=-0.97$) and nitrogen ($P<0.01$; $r=0.99$), while growth rate with phosphorus content ($P<0.05$; $r=0.97$) and food conversion efficiency with contents of organic carbon ($P<0.05$; $r=0.98$) and calcium ($P<0.01$; $r=-0.99$). Among *Areca*, *Elettaria*, and *Coffea* litters, *Areca*+*Elettaria*+*Coffea* was most preferred by *A. davisoni*, which was significantly correlated with organic carbon content ($P<0.05$; $r=0.98$) and food conversion efficiency with calcium content ($P<0.0001$; $r=0.99$). The food conversion efficiency, however, was the highest in millipedes fed with *Areca*+*Elettaria*. The present study demonstrated increased nitrogen and phosphorus contents

and decreased phenolic content and C/N ratio in fecal pellets of pill millipedes fed with plantation litter, and thus, these millipedes play an important role in leaf litter mineralization and soil enrichment in plantations Western Ghats.

Keywords Fecal pellets · Feeding preference · Food conversion efficiency · Growth · Leaf litter · Millipedes · Plantations · Western Ghats

Introduction

Soil macroinvertebrates are very important in improving the structure, content of organic matter, and nutrient elements of soil (Loranger-Merciris et al. 2007; Seeber et al. 2008). Synergistic function of saprophagous fauna and microflora in soil results in decomposition of organic matter and nutrient release (Kurzatkowski et al. 2004). Saprophagous invertebrates (e.g., millipedes, woodlice and Dipteran larvae) are known to ingest up to 20–100% of annual litter production (Tajovský et al. 1992). The excrements of saprophagous fauna consist of undigested plant residues, fine particulate organic matter, mineral particles and micro-organisms with higher pH (acidic to neutral), water holding capacity, and surface/volume ratio than standing dead litter (Kheirallah 1990; Tajovský et al. 1992; Lavelle and Spain 2001; Kurzatkowski et al. 2004; Seeber et al. 2008). Transformation of organic matter into rich inorganic nutrients and nutrient fluxes by saprophagous fauna in a specific habitat can be evaluated indirectly through the assessment of their abundance, population dynamics, diversity, succession, and energy budgets based on feeding and excretion (Anderson 1987; Pramanik et al. 2001; Loranger-Merciris et al. 2008). Several investigators demonstrated food preference in millipedes in temperate

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and tropical regimes (e.g., Schmidt 1952; Barlow 1957; van der Drift 1965; Ashwini and Sridhar 2005; Loranger-Merciris et al. 2008). Schmidt (1952) documented inter-specific differences in food preference in millipedes, which allows a maximum transformation of available food sources. Sakwa (1974) correlated palatability of decaying material to millipedes to nitrogen, carbohydrate, and moisture. Even though saprophagous faunal population density and metabolic rates are high in tropical forests, very little is known about their functional role (Lee 1991). Recently, Loranger-Merciris et al. (2008) studied millipede abundance in semi-evergreen dry tropical forest and related species richness and feeding preferences to litter nitrogen content.

Pill millipedes belonging to the genus *Arthrosphaera* are endemic to Southern India and Sri Lanka (Pocock 1899; Attems 1936). Recently, Ashwini and Sridhar (2008) reported a variety of *Arthrosphaera* species (Sphaerotheriidae) confined to the Western Ghat forests and plantations. Due to enormous increase in millipedes and earthworms in an organically managed mixed plantation, Ashwini and Sridhar (2005) studied the rate of ingestion of plantation litter, growth, and food conversion efficiency by *Arthrosphaera magna* Attems in relation to leaf chemistry in microcosm experiments. Interestingly, the rate of food ingestion of mixed litter by *A. magna* was higher than temperate and other tropical millipedes and so also the quantity of fecal pellet production (Lawrence and Samways 2003; Ashwini and Sridhar 2005). The main objective of the present study is to evaluate the leaf litter feeding preference and its conversion efficiency by two dominant pill millipede species (*Arthrosphaera dalyi* and *Arthrosphaera davisoni*) in plantations of the Western Ghats of India. The rate of leaf litter ingestion, growth, and production of fecal pellets were assessed in relation to chemistry of leaf litter and fecal pellets by microcosm experiments.

Materials and methods

Plantations

About 30-year-old Kadaba plantation spread over 2 ha at the Western Ghats (124 msl; 12°44' N, 75°29' E) receives rainfall up to 250–400 cm/annum, and temperature ranges between 21–22°C (minimum) and 34–36°C (maximum). The plantation consists of mainly palms of *Areca catechu* Linn. in association with two main tree species *Hopea parviflora* Bedd. and *Pongamia pinnata* (L.) Pierre as green manure and litter source. During post-monsoon season (October), *Areca* palms receive cow dung, spent slurry of biogas plant, and mixed green manure. In addition, leaf

litter accumulated on the plantation floor will be heaped at the plant bases. Plantation receives sprinkler irrigation (December through May), which is equivalent to 2.5 cm rainfall/day.

About 25-year-old Basrikallu plantation (1387 msl; 13°29' N, 75°40' E) at the Western Ghats has cool and humid climatic conditions with rainfall ranging from 400 to 600 cm/annum. The temperature ranges between 10–12°C (minimum) and 30–32°C (maximum). Three main plantations crops (*A. catechu* Linn., *Elettaria cardamomum* (L.) Maton, and *Coffea arabica* L.) are grown along with forest tree species (e.g., *Alstonia*, *Artocarpus*, *Hopea*, *Syzygium*, and *Terminalia*) for shade, green manure, and litter. This plantation has been organically managed using mixed leaf litter, green manure during post-monsoon (October), and sprinkler irrigation was followed during January to April.

Millipedes

A. dalyi Pocock and *A. davisoni* Pocock are the dominant pill millipedes of Kadaba and Basrikallu plantations, respectively. The litter feeding preference experiments on *A. dalyi* (September to October, 2005) and *A. davisoni* (September–October, 2006) were conducted during end of monsoon and early post-monsoon season. Adult millipedes collected from the plantations were acclimatized with partially decomposed leaf litter diets (*A. dalyi*: *Hopea*, *Pongamia*, and *Areca*; *A. davisoni*: *Areca*, *Elettaria*, and *Coffea*) up to 2 weeks (22±2°C) with 12-h light and dark regime in the laboratory.

Leaf litter

Three major leaf litters available in the vicinity of sampling location of millipedes in plantations were employed as diets. Freshly fallen leaf litter was spread over on the soil floor of the respective plantations up to 1 month during monsoon (August) for partial decomposition. A 4-day preliminary trial was performed offering leaf litter in seven combinations (*A. dalyi*: *Hopea*, *Pongamia*, *Areca*, *Hopea*+*Pongamia*, *Hopea*+*Areca*, *Pongamia*+*Areca*, and *Hopea*+*Pongamia*+*Areca*; *A. davisoni*: *Areca*, *Elettaria*, *Coffea*, *Areca*+*Elettaria*, *Areca*+*Coffea*, *Elettaria*+*Coffea*, and *Areca*+*Elettaria*+*Coffea*).

Feeding trials

A total of 15 g air-dried leaf litter was offered per replicate (single litter, 15 g; two litters, 7.5 g each; and three litters, 5 g each) in circular containers (20 cm diameter, 7 cm height) in five replicates. Acclimatized millipedes were starved up to 24 h prior to start feeding trials. For each replicate, four adult millipedes (two males and two females)

were weighed and marked on the second tergite with different colors for identification for subsequent weighing. They were allowed to feed on the moist leaf litter up to 4 days at 12-h light and dark regime in the laboratory ($22 \pm 2^\circ\text{C}$). The containers were covered with cotton cloth and on every day 10 ml water were sprinkled on the leaf litter in each container. After 4 days, animals were reweighed, fecal pellets were separated, and weight of remaining leaf litter was determined after air-drying. Leaf materials subjected to above conditions without animals served as control, and the weight loss in control sets by leaching or other means were deducted from experimental litter sets to determine litter consumption by millipedes.

Top three preferred litter combinations from the 4-day trial were selected for 4-week trial, and millipedes were fed with respective diets in five replicates as explained in 4-day trial. At every week, animals were reweighed, leaf litter were sorted out and air-dried and the remaining weight was determined to estimate the litter consumption rate, growth rate, and food conversion efficiency. Feeding trial was continued with decomposed leaf litter at the end of every week as described above. Animal weight prior to start feeding every week has been considered as initial weight for calculation. Fecal pellets collected in 4 weeks were pooled, air-dried, and preserved in refrigerator for chemical analysis.

The rate of consumption (litter ingested/day/animal), growth rate (weight gained/day/animal), and food conversion efficiency $\{[(\text{weight gained/day/animal})/(\text{litter ingested/day/animal})] \times 100\}$ were calculated (Waldbauer 1968).

Chemical analysis

Content of total phenolics, organic carbon, total nitrogen, total phosphorus, exchangeable calcium, exchangeable magnesium, and C/N ratio of air-dried leaf litter offered to the millipedes and air-dried fecal pellets in 4-week trials were assessed.

Total phenolics assay was performed after extracting sample (50–100 mg) twice with 50% methanol in a water bath at 95°C for 10 min (Rosset et al. 1982). The pooled extract was made up to 10 ml. An aliquot of 0.5 ml extract was mixed with 0.5 ml distilled water and treated with 5 ml Na_2CO_3 in 0.1 N NaOH. After 10 min, 0.5 ml Folin–Ciocalteus reagent was added, and optical density of the solution was read at 725 nm. Tannic acid was used as standard.

Organic carbon analysis was based on Walkley and Black's rapid-titration method (Jackson 1973). Organic carbon in 50–150 mg sample was oxidized to CO_2 by 1 N $\text{K}_2\text{Cr}_2\text{O}_7$. Leftover excess $\text{K}_2\text{Cr}_2\text{O}_7$ after oxidation was titrated against 0.5 N ferrous ammonium sulfate with diphenylamine indicator.

Total nitrogen was estimated by micro-Kjeldahl method (Jackson 1973). Sample (100 mg) was digested with 1 g catalytic mixture and 10 ml concentrated sulphuric acid. The digest was made up to 100 ml in standard flask with distilled water. A 10-ml aliquot was used for distillation in micro-Kjeldahl apparatus. The released ammonia was absorbed into known volume (10 ml) of 2% boric acid and titrated against 0.01 N HCl using mixed indicator.

Total phosphorus was extracted after ashing (200–300 mg) and diluting with concentrated HCl, filtered and estimated by ascorbic acid method (Jackson 1973). The absorbance was read at 880 nm using reagent blank as the reference. Known concentration of KH_2PO_4 was used to plot the calibration curve for estimation.

Exchangeable calcium and magnesium were determined based on the procedure outlined by Jackson (1973). Samples (500 mg) were digested in Kjeldahl digestion flask with 6 ml acid mixture and made up to 50 ml with distilled water. To detect calcium, 5 ml digest was diluted to 25 ml with distilled water in porcelain container, 10 ml 10% NaOH, and 0.5 g murexide indicator were added. The contents were titrated against standard EDTA until the color turn into violet. To determine calcium+magnesium, 5 ml digest were diluted to 25 ml with distilled water in porcelain container, 10 ml buffer (19 g NH_4Cl were dissolved in 142 ml NH_4OH and made up the volume to 250 ml with distilled water) and three to five drops of erichrome black-T indicator were added. The mixture was titrated against standard EDTA with constant stirring until the color turns into sky-blue. Magnesium was obtained on deduction of titer value of calcium from the titer value of calcium+magnesium.

Data analyses

Paired *t* test was employed to determine the difference in consumption rate of leaf litter (4-day trial), consumption rate, growth rate, and food conversion efficiency (4-month trial) and chemical composition between leaf litter and the fecal pellets of millipedes (StatSoft Inc. 1995). Pearson correlation was performed using GraphPad Prism version 4.0b for Macintosh, GraphPad Software, San Diego California, USA (<http://www.graphpad.com>) to determine the relationship between consumption rate, growth rate, and food conversion efficiency of millipedes vs. leaf chemistry (parameters: *p* values, two tailed; confidence intervals, 95%).

Results

In a 4-day trial, top three preferred litter combinations by *A. dalyi* were *Hopea*, *Hopea*+*Pongamia* and *Hopea*+*Pongamia*+*Areca* while by *A. davisoni* were *Areca*, *Areca*+

Elettaria and *Areca*+*Elettaria*+*Coffea* (Table 1). The consumption rate of top three preferred litters by millipedes significantly differed ($P<0.05$). Consumption of rest of the litter combinations was less than 5 mg/day per animal. In a 4-week trial, consumption of *Hopea*+*Pongamia*+*Areca* and *Hopea*+*Pongamia* by *A. dalyi* was highest initially, and it dropped steeply in former and gradually in latter (Fig. 1). The growth rate as well as food conversion efficiency attained highest in animals fed with *Hopea*+*Pongamia*. As seen in a 4-day trial, ingestion of *Areca*+*Elettaria*+*Coffea* was highest by *A. davisoni* and its consumption resulted in highest growth rate (Fig. 2). However, food conversion efficiency at the end of 4 week was highest on *Areca*+*Elettaria* diet. In both millipedes, consumption rate, growth rate, and food conversion efficiency significantly differed between most preferred litter and least preferred litter ($P<0.05$).

The content of phenolics decreased significantly between leaf litter and fecal pellets of *A. dalyi* (Table 2). Nitrogen and phosphorus contents were elevated in fecal pellets (except for the nitrogen content in animals fed with *Hopea*+*Pongamia*), while C/N ratio decreased. Magnesium content increased considerably in fecal pellets, while calcium content drastically decreased. In *A. davisoni*, the contents of phenolics and organic carbon in fecal pellets decreased significantly (except for the organic carbon in animals fed with *Areca*+*Elettaria*+*Coffea*). Nitrogen, phosphorus, and magnesium contents were elevated, while C/N ratio and calcium content decreased in fecal pellets of animals fed with most preferred litter combination *Areca*+*Elettaria*+*Coffea*.

Correlation of consumption rate by *A. dalyi* was negatively correlated with the organic carbon contents of all litter combinations (Table 3). Consumption rate of *Hopea* and *Hopea*+*Pongamia* was correlated with litter nitrogen content. The growth rate was positively correlated with phosphorus on consumption of *Hopea*+*Pongamia*.

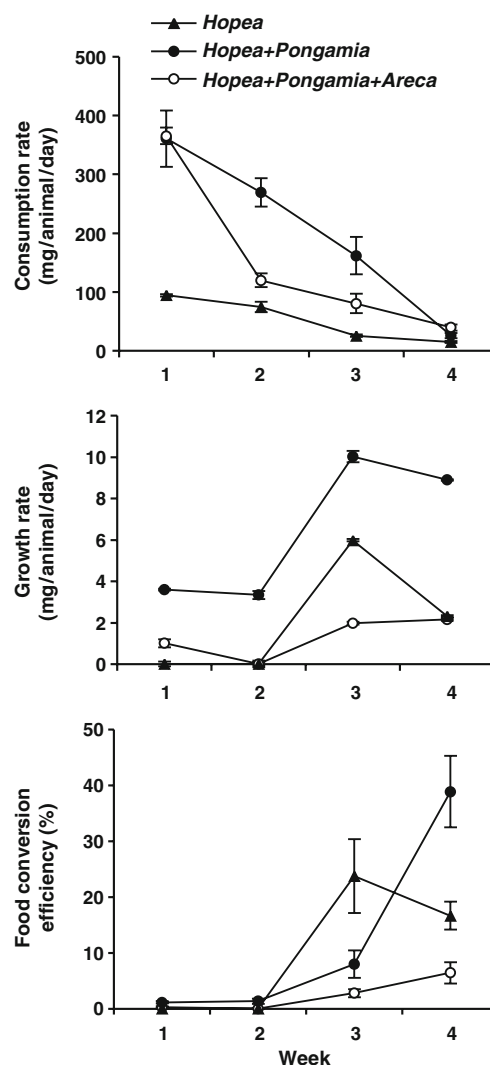


Fig. 1 Leaf litter consumption, growth, and food conversion efficiency of *Arthrosphaera dalyi* ($n=5$; mean \pm SE) (consumption rate, growth rate, and food conversion efficiencies between *Hopea* vs. *Hopea*+*Pongamia* and *Hopea*+*Pongamia*+*Areca* vs. *Hopea*+*Pongamia* were significantly different, $P<0.05$)

Table 1 Consumption rate of leaf litter by *Arthrosphaera dalyi* and *A. davisoni* in 4-day trial ($n=5$; mean \pm SD)

Diet	Consumption (mg/day/animal)
<i>Arthrosphaera dalyi</i>	
<i>Hopea</i>	105.56 \pm 11.52 ^a
<i>Hopea</i> + <i>Pongamia</i>	256.63 \pm 27.33 ^{bc}
<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	294.56 \pm 23.58 ^{bd}
<i>Arthrosphaera davisoni</i>	
<i>Areca</i>	51.38 \pm 6.05 ^a
<i>Areca</i> + <i>Elettaria</i>	28.20 \pm 3.26 ^{bc}
<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	101.15 \pm 21.62 ^{bd}

Data with different letters across the rows are significantly differed ($P<0.05$)

The food conversion efficiency in most preferred litter combination (*Hopea*+*Pongamia*+*Areca*) was significantly correlated with organic carbon, nitrogen, and calcium contents. In *A. davisoni*, consumption of *Areca* was significantly correlated with organic carbon and phosphorus content (Table 3). The food conversion efficiency was significantly correlated with nitrogen content of *Areca*. Food consumption and food conversion efficiency were significantly correlated with organic carbon and calcium content of *Areca*+*Elettaria*+*Coffea*.

In both millipedes, the rates of food consumption, growth, and food conversion efficiencies were not significantly correlated with the contents of phenolics and magnesium.

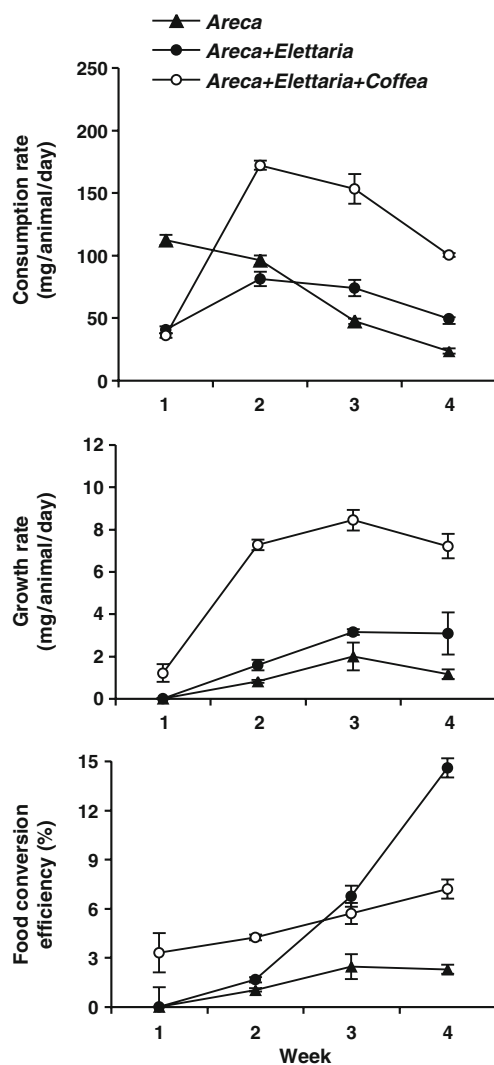


Fig. 2 Leaf litter consumption, growth, and food conversion efficiency of *Arthrosphaera davisoni* ($n=5$; mean \pm SE) (consumption rate, growth rate, and food conversion efficiencies between *Areca* vs. *Areca*+*Elettaria*+*Coffea* and *Areca*+*Elettaria* vs. *Areca*+*Elettaria*+*Coffea* were significantly different, $P<0.05$)

Discussion

Variation in quantity and quality of plant litter has been demonstrated to influence organic matter mineralization by soil macrofauna (Warren and Zou 2002; Seeber et al. 2008). Leaf litter consumption by millipedes mainly depends on the nutritive value and extent of decomposition (Schmidt 1952; Kheirallah 1979; Loranger-Merciris et al. 2008). Sileshi and Mafongoya (2007) showed spatial aggregation of millipedes in heterogeneous organic resource. Warren and Zou (2002) significantly correlated biomass of millipedes to the nitrogen content and C/N ratio in *Leucaena* plantations of Puerto Rico. Recently, Loranger-Merciris et al. (2008) also demonstrated high

feeding preferences of nitrogen-rich leaf litter by three millipede species in semi-evergreen tropical dry forest of Guadeloupe.

Our study supports the hypothesis of preference of leaf litter with high nitrogen content and low C/N ratio by pill millipedes *A. dalyi* and *A. davisoni*. Consumption of *Hopea* by *A. dalyi* was least while *Hopea*+*Pongamia* was highest in the 4-week trial, which resulted in elevated growth as well as food conversion efficiency. *Hopea* was least preferred by *A. dalyi* in 4-week trial, possibly due to highest phenolic content and C/N ratio, and least nitrogen and phosphorus contents. On the contrary, *Hopea*+*Pongamia* was preferred due to low phenolic content and C/N ratio and high nitrogen and calcium contents. However, *A. davisoni* preferred *Areca*+*Elettaria*+*Coffea* in spite of high phenolic content, which may harbor suitable gut microflora-producing phenol oxidases (Loranger-Merciris et al. 2007). It is interesting to note that food conversion efficiency of *A. davisoni* was highest in *Areca*+*Elettaria* diet, although it was moderately preferred.

Tannins constitute significant portion (40%) of forest litter and leads to retard nutrient cycling by invertebrates and microbes in soils (Kraus et al. 2003). Sakwa (1974) opined that polyphenol and tannin contents in fresh leaf litter decreased the attraction to millipedes. Sileshi and Mafongoya (2007) showed more abundance of millipedes in organic matter with high lignin+polyphenol to nitrogen ratios. Similarly, Loranger-Merciris et al. (2007, 2008) demonstrated low palatability of leaf litter to millipedes due to high quantity of phenols and less nitrogen content. The millipede, *Jonespeltis splendidus* preferred leaf litter (*Artocarpus*, *Macaranga*, and *Terminalia*) with advanced stage of decay with low phenolics and high sugar content (Devi and Prabhoo 1990). Decomposition and microbial activity substantially lower the litter phenolic contents (Edwards et al. 1970; Satchell 1974), and thus, pill millipede *A. magna* prefers decomposed over fresh leaf litter (Ashwini and Sridhar 2005).

Although large bodied tropical millipedes showed high ingestion and throughput rates, they do not have high assimilation efficiency as they rely on low-quality diets (Striganova and Prishutova 1990; Dangerfield and Milner 1993, 1996). As the climatic changes in humid tropics are less extreme, litter chemistry assumes importance in decomposition processes (Tian et al. 1993; Henegan et al. 1999; González et al. 2001). The qualities of leaf litter in tropical region influence the millipede population and, in turn, the rate of litter mineralization (Tian et al. 1993; Loranger-Merciris et al. 2007, 2008). Even though partially decomposed mixed litter was palatable to both pill millipedes in our study, food conversion efficiency of *A. dalyi* is about threefold higher than *A. davisoni*. It is possible that *A. davisoni* prefers other mixed litter

Table 2 Chemical composition of leaf litter offered and fecal pellets of *Arthrosphaera dalyi* and *A. davisoni* ($n=5$; mean \pm SD)

Composition	Diet	Leaf litter	Fecal pellets
<i>Arthrosphaera dalyi</i>			
Phenolics (%)	<i>Hopea</i>	17.80 \pm 1.74 ^a	2.69 \pm 0.18 ^{b*}
	<i>Hopea</i> + <i>Pongamia</i>	1.18 \pm 0.29 ^a	0.69 \pm 0.34 ^{b*}
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	2.55 \pm 0.09 ^a	0.85 \pm 0.46 ^{b*}
Organic carbon (%)	<i>Hopea</i>	18.20 \pm 1.66 ^a	17.83 \pm 1.13 ^a
	<i>Hopea</i> + <i>Pongamia</i>	18.65 \pm 2.38 ^a	20.29 \pm 3.26 ^a
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	20.67 \pm 1.18 ^a	20.60 \pm 1.05 ^a
Nitrogen (%)	<i>Hopea</i>	1.49 \pm 0.08 ^a	2.68 \pm 0.83 ^a
	<i>Hopea</i> + <i>Pongamia</i>	4.53 \pm 0.21 ^a	3.74 \pm 0.26 ^a
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	3.41 \pm 0.08 ^a	4.50 \pm 2.45 ^a
C/N Ratio	<i>Hopea</i>	12.18 \pm 0.17 ^a	7.11 \pm 2.17 ^{b*}
	<i>Hopea</i> + <i>Pongamia</i>	6.19 \pm 0.82 ^a	5.41 \pm 0.63 ^a
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	7.46 \pm 0.96 ^a	5.40 \pm 2.26 ^a
Phosphorus (%)	<i>Hopea</i>	0.052 \pm 0.01 ^a	0.158 \pm 0.11 ^a
	<i>Hopea</i> + <i>Pongamia</i>	0.055 \pm 0.04 ^a	0.269 \pm 0.06 ^a
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	0.148 \pm 0.02 ^a	0.401 \pm 0.07 ^a
Calcium (%)	<i>Hopea</i>	6.24 \pm 0.17 ^a	4.07 \pm 0.21 ^a
	<i>Hopea</i> + <i>Pongamia</i>	5.60 \pm 0.16 ^a	3.97 \pm 0.51 ^{b*}
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	4.77 \pm 0.09 ^a	2.93 \pm 0.34 ^{b*}
Magnesium (%)	<i>Hopea</i>	1.44 \pm 0.41 ^a	2.00 \pm 0.38 ^{b*}
	<i>Hopea</i> + <i>Pongamia</i>	1.25 \pm 0.16 ^a	1.88 \pm 0.13 ^a
	<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	1.15 \pm 0.02 ^a	1.46 \pm 0.27 ^a
<i>Arthrosphaera davisoni</i>			
Phenolics (%)	<i>Areca</i>	4.80 \pm 0.45 ^a	0.89 \pm 0.07 ^{b***}
	<i>Areca</i> + <i>Elettaria</i>	2.97 \pm 0.21 ^a	0.53 \pm 0.07 ^{b***}
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	9.07 \pm 0.24 ^a	3.26 \pm 0.16 ^{b***}
Organic carbon (%)	<i>Areca</i>	24.54 \pm 0.70 ^a	16.57 \pm 0.66 ^{b***}
	<i>Areca</i> + <i>Elettaria</i>	18.69 \pm 0.37 ^a	16.31 \pm 0.97 ^{b***}
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	19.21 \pm 0.36 ^a	22.16 \pm 0.55 ^{b**}
Nitrogen (%)	<i>Areca</i>	2.48 \pm 0.48 ^a	1.46 \pm 0.38 ^{b**}
	<i>Areca</i> + <i>Elettaria</i>	1.71 \pm 0.28 ^a	1.81 \pm 0.25 ^a
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	2.73 \pm 0.26 ^a	3.41 \pm 0.29 ^{b*}
C/N Ratio	<i>Areca</i>	9.91 \pm 3.19 ^a	12.04 \pm 3.88 ^{b*}
	<i>Areca</i> + <i>Elettaria</i>	10.96 \pm 1.10 ^a	9.09 \pm 1.24 ^{b***}
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	7.04 \pm 2.62 ^a	6.52 \pm 0.53 ^{b***}
Phosphorus (%)	<i>Areca</i>	0.285 \pm 0.01 ^a	0.213 \pm 0.01 ^{b*}
	<i>Areca</i> + <i>Elettaria</i>	0.169 \pm 0.01 ^a	0.260 \pm 0.02 ^{b*}
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	0.223 \pm 0.03 ^a	0.310 \pm 0.04 ^a
Calcium (%)	<i>Areca</i>	3.68 \pm 0.35 ^a	1.02 \pm 0.07 ^{b**}
	<i>Areca</i> + <i>Elettaria</i>	2.31 \pm 0.15 ^a	1.01 \pm 0.06 ^{b**}
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	2.15 \pm 0.19 ^a	2.12 \pm 0.15 ^{b***}
Magnesium (%)	<i>Areca</i>	0.96 \pm 0.19 ^a	0.47 \pm 0.02 ^{b*}
	<i>Areca</i> + <i>Elettaria</i>	0.58 \pm 0.13 ^a	0.55 \pm 0.02 ^a
	<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	0.54 \pm 0.10 ^a	0.90 \pm 0.10 ^{b**}

* $P<0.05$; ** $P<0.01$; *** $P<0.001$

combination than we offered in the laboratory to attain elevated growth and food conversion efficiency. Our study corroborates with earlier reports that the quality of leaf litter is important in enhancing the growth and food

conversion efficiency of millipedes that, in turn, leads to leaf litter mineralization and soil enrichment (Ashwini and Sridhar 2005; Loranger-Merciris et al. 2007, 2008; Seeber et al. 2008).

Table 3 Pearson correlation coefficients between consumption, growth, and food conversion efficiencies of *Arthrosphaera dalyi* and *A. davisoni* against leaf litter chemistry (significant *P* values in paranthesis)

Diet	Total phenolics	Organic carbon	Total nitrogen	Total phosphorus	Calcium	Magnesium
<i>Arthrosphaera dalyi</i>						
Consumption						
<i>Hopea</i>	0.351	−1.00*** (<0.0001)	−0.9861* (0.0139)	−0.3383	0.4773	−0.06253
<i>Hopea</i> + <i>Pongamia</i>	−0.4873	−0.9767* (0.0233)	0.9985** (0.0015)	−0.8582	0.8954	−0.2461
<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	−0.5168	−0.96* (0.04)	−0.8727	−0.5471	0.8938	−0.1108
Growth						
<i>Hopea</i>	0.4788	0.6593	0.7689	−0.4617	0.3527	−0.7139
<i>Hopea</i> + <i>Pongamia</i>	0.9399	0.598	−0.7206	0.976* (0.024)	−0.3856	−0.4484
<i>Hopea</i> + <i>Pongamia</i> + <i>Areca</i>	0.5578	0.8942	0.7966	0.5397	−0.8141	0.02759
Food conversion efficiency						
<i>Areca</i> + <i>Pongamia</i> + <i>Hopea</i>	0.1265	0.9913** (0.0087)	0.9956** (0.0044)	0.1672	−0.9987** (0.0013)	0.5032
<i>Pongamia</i> + <i>Hopea</i>	0.1013	0.9818* (0.0182)	−0.9376	0.5893	−0.9985** (0.0015)	0.61
<i>Hopea</i>	0.1011	0.8996	0.956* (0.044)	−0.1027	−0.03762	−0.387
<i>Arthrosphaera davisoni</i>						
Consumption						
<i>Areca</i>	−0.4808	−0.9602* (0.0398)	−0.7527	0.9588* (0.0412)	−0.4087	0.9451
<i>Areca</i> + <i>Elettaria</i>	0.566	−0.5697	−0.8293	−0.2136	−0.8155	0.8076
<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	0.6167	0.9862* (0.0138)	0.2959	0.8369	−0.1488	0.6417
Growth						
<i>Areca</i>	−0.8742	−0.5989	−0.09084	0.8417	0.3337	0.4586
<i>Areca</i> + <i>Elettaria</i>	−0.8282	−0.4453	0.243	0.9158	0.435	−0.1019
<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	−0.1762	0.5333	0.9095	0.1494	0.6382	−0.1438
Food conversion efficiency						
<i>Areca</i>	−0.1398	0.8059	1.00*** (<0.0001)	−0.5711	0.9119	−0.9233
<i>Areca</i> + <i>Elettaria</i>	−0.7622	0.2497	0.7241	0.5318	0.7913	−0.6507
<i>Areca</i> + <i>Elettaria</i> + <i>Coffea</i>	−0.8718	−0.3139	0.8992	−0.6681	0.9999*** (<0.0001)	−0.8545

P*<0.05; *P*<0.01; ****P*<0.001

Leaf litter ingestion and fecal pellet production by millipedes occur mainly during 2 months of wet season in Southern Africa (Dangerfield and Telford 1991), which enhance decomposition of litter standing crop to a significant proportion (Dangerfield and Milner 1993). Millipede feces consist of pulverized litter, minerals, and high microbial load (Wallwork 1970; Jenson 1974). The rich organominerals in millipede fecal pellets accelerate humification of litter strata (Loranger et al. 2003). Ashwini and Sridhar (2002, 2006) found spongy, soft, and black humic soil in *Areca* and cocoa mixed plantations with abundant population of *A. magna* during post-monsoon season. Organic matter in the fecal pellets decreased considerably compared to the leaf litter ingested (Ashwini and Sridhar 2005). In our study, between leaf litter and fecal pellets, in most instances, phenolics, C/N ratio, calcium, and magnesium contents decreased, while nitrogen and phosphorus contents elevated. This shows enrichment of fecal pellets with nitrogen and phosphorus contents and acquisition of calcium and magnesium by the pill milli-

pedes *A. dalyi* and *A. davisoni*. Lyford (1943) demonstrated that the leaf litter palatability to millipedes depends on the leaf litter calcium content, and Ashwini and Sridhar (2006) also correlated pill millipede abundance and biomass to soil calcium content in Western Ghat region. As pill millipede population (*A. dalyi* and *A. davisoni*) is abundant and adapted to mixed plantations of Kadaba and Basrikallu of the Western Ghats, they are very important saprophagous fauna to develop future sustainable organic farming and plantation management practices. Further studies, particularly the field trials, are necessary to understand more precisely the roles of these pill millipedes in soil enrichment in forests and plantations of Western Ghats.

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