An assemblage of terrestrial isopods (Crustacea) in southern Brazil and its contribution to leaf litter processing [1]

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ABSTRACT. We present an assemblage of terrestrial isopods in Parque Estadual de Itapuã, southern Brazil, and estimate the contribution of two species to the leaf litter processing. After one year of sampling, we obtained 3748 individuals of six species and four eco-morphologic groups (in order of abundance): *Balloniscus glaber* Araujo & Zardo, 1995, *Atlantoscia floridana* (van Name, 1940), *Pseudodiploexochus tabularis* (Giambiagi de Calabrese, 1939), *Trichorhina* sp., *Alboscia itapuensis* Araujo & Quadros, 2005 and *Novamundoniscus gracilis* Lopes & Araujo, 2003. Total monthly density corresponded to 368 individuals per square meter. The species *A. itapuensis* and *N. gracilis* represented less than 1% of total individuals. All the others showed aggregated distribution. *Atlantoscia floridana* and *B. glaber* had the highest proportion of individuals occurring together (88%) and a significant species association. Their monthly biomass averaged 4.92 kg ha^{-1} for *B. glaber* and 0.97 kg ha^{-1} for *A. floridana*. Consumption rates, obtained in the lab (in mg mg^{-1} day^{-1}) were 0.34 ± 0.04 and 0.70 ± 0.18 for *B. glaber* and *A. floridana*, respectively and assimilation efficiency was about 30%. We estimated that both species together could process 860 kg leaves ha^{-1} year^{-1}.
KEY WORDS. Aggregation; eco-morphological groups; feeding rates; Isopoda; species association.

RESUMO. **Uma assembléia de isópodos terrestres (Crustacea) no sul do Brasil e sua contribuição para o processamento da serapilheira.** Neste estudo é descrita uma assembléia de isópodos terrestres no Parque Estadual de Itapuã e estimada a contribuição de duas espécies para o processamento da serapilheira. Após um ano, foram obtidos 3748 indivíduos, correspondendo a seis espécies de quatro grupos eco-morfológicos (em ordem de abundância): *Balloniscus glaber* Araujo & Zardo, 1995, *Atlantoscia floridana* (van Name, 1940), *Pseudodiploexochus tabularis* (Giambiagi de Calabrese, 1939), *Trichorhina* sp., *Alboscia itapuensis* Araujo & Quadros, 2005 e *Novamundoniscus gracilis* Lopes & Araujo, 2003. A densidade mensal média correspondeu a 368 indivíduos por metro quadrado. As espécies *A. itapuensis* e *N. gracilis* representaram menos que 1% do total de indivíduos. As outras quatro espécies mostraram distribuição agregada. *Atlantoscia floridana* e *B. glaber* apresentaram 88% de indivíduos ocorrendo juntos. A biomassa mensal destas duas espécies foi de 4,92 kg ha^{-1} (*B. glaber*) e 0,97 kg ha^{-1} (*A. floridana*). As taxas de consumo, em mg mg^{-1} dia^{-1} foram 0,34 ± 0,04 (*B. glaber*) e 0,70 ± 0,18 (*A. floridana*). A eficiência de assimilação foi em torno de 30%. Foi estimado que as duas espécies juntas são capazes de processar 860 kg folhas ha^{-1} ano^{-1}.
PALAVRAS-CHAVE. Agregação; associação entre espécies; grupos eco-morfológicos; Isopoda; taxas de alimentação.

Terrestrial isopods (Crustacea, Oniscidea) are soil inhabitants widespread through a variety of habitats. Inventory and diversity studies have been conducted, and about 3,600 species are known (SCHMALFUSS 2003). Regarding oniscidean assemblages of coexisting species, some patterns can be drawn: they are usually composed by few species (up to 10) (HASSALL & DANGERFIELD 1989, HORNUNG & WARBURG 1996, LYMBERAKIS et al. 2003, ZIMMER 2003, LOPES et al. 2005), endemics and widely distributed (JUDD & HORWITZ 2003, LOPES et al. 2005). The spatial distribution is not homogeneous (HORNUNG & WARBURG 1995, JUDAS & HAUSER 1998, GONGALSKY et al. 2005), and may lead to strong species association (HASSALL & DANGERFIELD 1989, ZIMMER 2003) and there is a high fluctuation in density along the time (ZIMMER 2003, LYMBERAKIS et al. 2003).

Syntopic oniscideans often show contrasting morphological and behavioral characteristics and belong to different eco-morphological groups (SCHMALFUSS 1984) and may avoid competition through species-specific utilization of resources, as for example, food (ZIMMER 2003). The classification into eco-morphological groups, proposed by SCHMALFUSS (1984), takes into

account their anti-predatory strategies, microhabitat use and body morphology/size, grouping the isopods in "runners', "clingers", "rollers", "creepers", "spiny forms" and "non-conformists".

Although still poorly studied, terrestrial isopods play an important ecological role in the soil, as members of the detritivore community. Especially in forests, detritivory is of great importance, as the litter layer provides the major source of decomposable organic matter which supplies the forest growth (WEBB 1977, FÖRSTER *et al.* 2006). Detritivorous macroarthropods as isopods, diplopods and termites participate mainly in the processing of litter, by the mechanical breakdown and comminuting of the leaves (WEBB 1977), and are known to be responsible for the processing of up to 40% of the annual leaf fall is some environments (MATSUMOTO & ABE 1979, DANGERFIELD & MILNER 1996, DAVID & GILLON 2002). As they generally have a low efficiency of assimilation, most of the ingested leaf litter returns to the soil as feces, which are chemically and physically different from the original vegetal material (HASSALL & RUSHTON 1982, SCHEU & WOLTERS 1991, ZIMMER 2002). The feces are more suitable to microbial colonization and constitute a source of food for other soil organisms (SCHEU & WOLTERS 1991, DAVID & GILLON 2002).

In the south of Brazil there is a good knowledge of the oniscidean fauna. The description of new species (ARAUJO & ZARDO 1995, LOPES & ARAUJO 2003, ARAUJO & QUADROS 2005) as well as biogeographical surveys (LOPES *et al.* 2005) and diversity inventories (ARAUJO *et al.* 1996, ALMERÃO *et al.* 2006) have been conducted, revealing a considerable heterogeneity in species richness, diversity and composition (LOPES *et al.* 2005).

As pointed by LEWINSOHN *et al.* (2005), invertebrate conservation depends on conserving entire habitats and on a more thorough understanding of their roles in maintaining ecosystem processes. Therefore, in the present study we provide an estimative of the participation of syntopic oniscideans in the soil processes, in addition to the description of an assemblage. Based on size and abundance, we have elected the two most representative species for a laboratory evaluation of feeding rates and the subsequent estimative of their contribution to litter processing in a subtropical forest of southern Brazil.

MATERIAL AND METHODS

Sampling

We selected a site of 216 m² next to "Trilha da Onça" on a hill slope near the lagoon beach "Praia da Onça" (30º34'S 51º05'W) in the Parque Estadual de Itapuã (PEI). The vegetation community is a secondary, semi-deciduous forest. For a more detailed description of the study site see ALMERÃO *et al.* (2006) and QUADROS & ARAUJO (2007). The site of 216 m² was divided in 12 consecutive sectors (18 m²). Monthly, from May 2004 to April 2005, we sorted and extracted one sample from each sector, totaling 144 samples in one year. Although previous studies used the hand-search method for the collection of

animals, we chose to sample a known area, using a circular bottom-less recipient of 707 cm². From the interior of this recipient, we transferred all vegetal material and the top soil layer (≈3 cm deep) to plastic bags to be hand-searched in the lab. This method allows the capture of the smallest individuals as well as the largest (see ARAUJO & BOND-BUCKUP 2005, QUADROS & ARAUJO 2007), the disadvantage being the time-consuming task of examining all the contents.

Assemblage description

After the identification and counting of the individuals, the species were classified according to size and eco-morphological groups. Size classification followed BEGON *et al.* (2005): Mesofauna comprises animals with up to 2 mm body width, asnd Macrofauna comprises animals with > 2 mm and < 20 mm. The classification of terrestrial isopods into eco-morphological groups was according to SCHMALLFUSS (1984).

An analysis of the variance/mean ratio for each species density suggested a clumped distribution for all species (variance > mean). Species density was grouped in seasons, transformed ($Log_{10} + 1$) to minimize the effects of the clumped distribution (ARAUJO & BOND-BUCKUP 2005) and compared with ANOVA. Average density of *Atlantoscia floridana* (van Name, 1940) and *Balloniscus glaber* Araujo & Zardo, 1995 is published elsewhere (QUADROS & ARAUJO 2007).

Aggregation was quantified monthly through the Morisita's Index of Dispersion (MID) as follow: MID = $[n(\Sigma i^2-\Sigma i)/((\Sigma i)^2-\Sigma i)]$, where n = 12 (number of samples per month) and i = number of individuals per sample (ELLIOT 1983). This index was chosen because it is independent of the number of individuals (ELLIOT 1983), which was highly variable in this study.

Association between pairs of species was calculated in two ways, both described in SOUTHWOOD & HENDERSON (2000). First we constructed presence-absence contingency tables for each pair of species. Then, the χ^2 statistics is calculated for each pair: $\chi^2 = [n[|ad–bc|-(n/2)]^2]/[(a+c)(b+d)(a+b)(c+d)]$, where the letters a, b, c and d correspond to the number of samples with: both species (a); only species B (b); only species A (c) and none species (d). Deviation from random distribution was tested with Fisher's exact test, as recommended in cases where expected numbers are lower than five (SOUTHWOOD & HENDERSON 2000).

After identifying significant χ^2, we calculated the coefficient of mean square contingency (C_{AB}) to give a quantitative value for comparison with other species: $C_{AB} = [sqrt(\chi^2/(n + \chi^2))]$, where C_{AB} = coefficient of association between species A and B; n = total number of occurrences and χ^2 as calculated above (SOUTHWOOD & HENDERSON 2000).

The second index was the proportion of individuals occurring together (I_{AB}): $I_{AB} = 2[(J/(A+B)) – 0.5]$, where J = number of individuals of A and B in samples where both species are present and A and B = total individuals of A and B in all samples (SOUTHWOOD & HENDERSON 2000).

Also, intraspecific and interespecific aggregation were calculated as in PRESA ABÓS *et al.* (2006). Intraspecific aggrega-

tion (J_A) is given by $J_A = [(V_A/m_A{}^2) - (1/m_A)]$, where V_A = variance and m_A = mean number of individuals of species A per sample. Interespecific aggregation (L_{AB}) is L_{AB} = [covariance$_{AB}$/($m_A m_B$)], where m_A and m_B = mean number of species A and B per sample, respectively. A value of $L_{AB} > 0$ indicates a positive association and $L_{AB} < 0$ indicates a negative association (Presa Abós *et al.* 2006). The relationship between these two measures was calculated as: $S_{AB} = |(J_A-1)(J_B-1)|/[(L_{AB}-1)^2]$. A value of $S_{AB} > 1$ indicates that intraspecific aggregation is stronger then interespecific aggregation (Presa Abós *et al.* 2006).

Biomass and estimative of leaf litter processing

Due to their abundance and size only *A. floridana* and *B. glaber* were chosen for biomass and litter processing estimates. We obtained their biomass by drying all specimens at 80°C for 48 h and weighing on an analytical balance (precision of 0.1 mg).

Collection of live animals occurred in June/July 2004. They were transported to the laboratory and maintained at ambient temperature ($\cong$ 18°C) and photoperiod (10:14 L:D) until experimentation. We also collected leaf litter to be offered as food during the experiments.

The experimental units consisted of small plastic boxes (8 cm diameter) containing cotton moistened with distilled water and 125 ± 11 mg of leaf litter (dry weight) as food. About 100 adult individuals of each species were distributed into the experimental units, totaling 50 units with two *B. glaber* individuals and 25 units with four *A. floridana* individuals. To control for autogenic changes in food weight, 20 units were set in the same conditions and maintained without the animals; the average percentage of weight lost in the controls was calculated and discounted from the amount consumed in each unit at the end of the experiment.

The units were checked daily for dead individuals and to provide water. Whenever occurred death, the unit was excluded from the analysis. The experiment was ended when approximately 50% of the food was consumed, which took from 7 to 14 days. Overall, 45 units of *B. glaber* and 14 units of *A. floridana* could be analyzed, this difference been due to mortality that occurred along the experiment. In the end, the animals, feces and the remaining leaf litter were separated in glass containers, oven dried and weighed and the rates calculated. Consumption rate (CR) and egestion rate (ER) were calculated on a dry weight basis, as mg food ingested per mg body weight per day and as mg feces produced per mg body weight per day, respectively. Assimilation efficiency (AE, %) is the percentage assimilated from the amount consumed.

The estimative of the annual amount of leaf litter processed by *A. floridana* and *B. glaber* was obtained by multiplying the mean CR and ER by the mean biomass in the field, and compared to the annual litterfall budget of the studied environment, which was obtained from the literature. Otherwise stated, all values shown refer to mean ± 95% confidence intervals.

RESULTS

After one year we obtained 3748 individuals of six species in five families (Tab. I). *Balloniscus glaber*, *Atlantoscia floridana* and *Pseudodiploexochus tabularis* (Giambiagi de Calabrese, 1939) (in order) were the commonest species, being present in ca. 80% of total samples and representing 93% of total individuals (Tab. I). Four of the six eco-morphological groups were present: a "runner", a "clinger", a "conglobating" and two "creepers" species (Tab. I). The group of *Novamundoniscus gracilis* Lopes & Araujo, 2003 could not be determined, however we believe it is probably a "runner". In relation to size there was also a wide variation: from mesofaunal representatives of 2 mm as *Alboscia itapuensis* Araujo & Quadros, 2005, to macrofaunal species of up to 13 mm in length, as *B. glaber* (Tab. I).

Trichorhina sp. could not be identified; it is probably a new species to science and probably the same referred by Lopes *et al.* (2005).

In average, each sample contained three species and 25 ± 3 individuals. Total number of individuals captured per month was in average 309 ± 42, corresponding to 368 ind m^{-2}. The abundance of each species per month is shown in figure 1. *Alboscia itapuensis* and *N. gracilis* were found mostly in winter and spring, in very low numbers: their densities were 1.3 ± 0.7 and 1 ± 0.8 ind m^{-2}, respectively. The other four species were present through the year (Fig. 1). Density of *Trichorhina* sp. was also low, 22 ± 8 ind m^{-2}, whereas the other three species were present in much higher densities: 96 ± 21 ind m^{-2} for *P. tabularis*, 113 ± 22 ind m^{-2} for *A. floridana* and 133 ± 17 ind m^{-2} for *B. glaber*. Only *A. floridana* showed different densities between seasons (see Quadros & Araujo 2007).
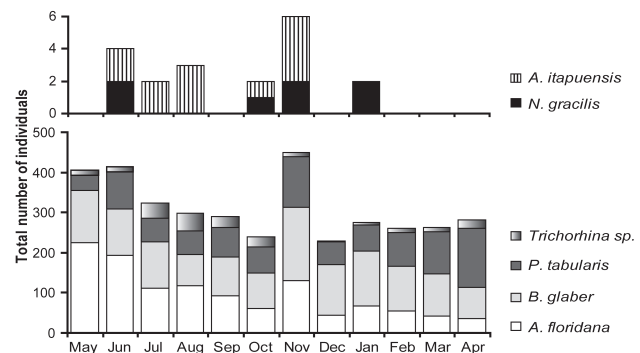

Figure 1. Total number of individuals of terrestrial isopods captured monthly at Parque Estadual de Itapuã, from May 2004 to April 2005.

As *A. itapuensis* and *N. gracilis* represented less than 1% of total individuals, they were excluded from dispersion and association analyses. All the others showed aggregated distribution (MID > 1), which varied in intensity along the year (Fig.

Table I. Composition of the studied terrestrial isopod assemblage at Parque Estadual de Itapuã. (% TN) percentage of total number of individuals captured, (% TS) occurrence of the species in percentage of total samples. References are indicated by superscript numbers: 1) Araujo & Zardo (1995), 2) ARAUJO et al. (1996), 3) LOPES & ARAUJO (2003), 4) TAITI & FERRARA (1979), 5) FERRARA & TAITI (1981), 6) LOPES et al. (2001), 7) ARAUJO & QUADROS (2005), 8) LOPES et al. (2005).

Taxa	% TN	% TS	Body length and size classification	Eco-morphological group	Known geographic distribution
Macrofauna					
Balloniscidae					
Balloniscus glaber	36.1	93.7	13.3 mm (male), 13.5 mm (female)[1]	Clinger	Southern Brazil (RS) [1]
Philosciidae					
Atlantoscia floridana	31.2	83.3	5.2 mm (male), 7 mm (female)[2]	Runner	South America [2]
Mesofauna					
Dubioniscidae					
Novamundoniscus gracilis	0.3	4.2	3.6 mm (male), 4.2 mm (female)[3]	Undetermined	Southern Brazil (RS) [3]
Armadillidae					
Pseudodiploexochus tabularis	26.1	71.5	Diameter in conglobating[4] = 2 mm	Conglobating	South Africa [4]; Ascension Island[5]; Southern Brazil (RS) [6]
Philosciidae					
Alboscia itapuensis	0.3	8.3	2 mm (male), 2.8 mm (female)[7]	Creeper	Southern Brazil (RS) [7]
Platyarthridae					
Trichorhina sp.	6.0	39.0	3 mm	Creeper	Unknown; probably Southern Brazil (RS) [8]

2). *Trichorhina* sp. showed the most intense aggregation, evidenced both by the MID and the intraspecific aggregation index (Tab. II). For both *Trichorhina* sp. and *P. tabularis* aggregation was stronger during winter and summer (Fig. 2). For *A. floridana* there was an increase in aggregation during the hottest months in summer. *Balloniscus glaber* showed no pronounced differences along the year (Fig. 2) and it had the lowest index of intraspecific aggregation (Tab. II).
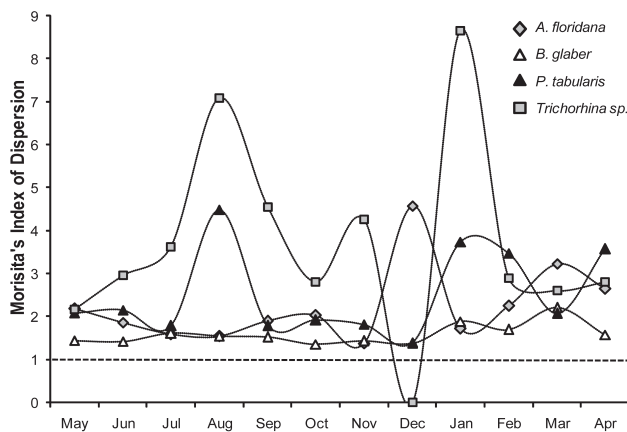

Figure 2. Isopod spatial distribution (Morisita's index of dispersion) in Parque Estadual de Itapuã, from May 2004 to April 2005. Values higher than 1 indicate an aggregate (contagious) distribution.

Atlantoscia floridana and *B. glaber* had the highest proportion of individuals occurring together (88%) and a significant species association (Tab. III). Also, *P. tabularis* x *B. glaber* and *P. tabularis* x *A. floridana* species pairs shared a high proportion of individuals (Tab. III). Interespecific aggregation was higher for *Trichorhina* sp. x *P. tabularis* species pair; however, in all cases intraspecific aggregation was stronger than interespecific (Tab. II).

Biomass

With the exception of May and June 2004, biomass of *B. glaber* was higher than *A. floridana* (Fig. 3). The average biomass of *A. floridana* corresponded to 0.97 kg ha^{-1} (± 0.2) and for *B. glaber* it was 4.9 kg ha^{-1} (± 0.1). Considering the sum of the species, average biomass was 590 mg m^{-2}, i.e. 5.90 kg ha^{-1} (± 0.8). As can be seen in figure 3, there was a significant difference between spring 2004 (Sep-Nov) and autumn 2005 (Mar-May) where total biomass was 6.9 kg ha^{-1} (± 1.4) and 3.8 kg ha^{-1} (± 1.6), respectively. *Balloniscus glaber* accounted for 87% of the total biomass. Total biomass of *A. floridana* and *B. glaber*, on a fresh weight (FW) basis, corresponded to ≈ 2560 mg m^{-2}.

Leaf litter processing

Atlantoscia floridana presented higher CR and ER than B. glaber, the assimilation efficiency being the same for both species, about 30% (Tab. IV). In table V we listed some annual litterfall estimative gathered from the literature. Considering only the leaf portion, we could expect an annual mean input of 5275 kg ha^{-1} in deciduous and semi-deciduous forests of South and Southeast Brazil (Tab. V). By multiplying the feeding rates

Table II. On the left, measure of intraspecific aggregation (J). On the right, measure of interespecific aggregation (L_{AB}) in the upper triangle and the strength of intra- versus interespecific aggregation (S_{AB}) in the bottom triangle.

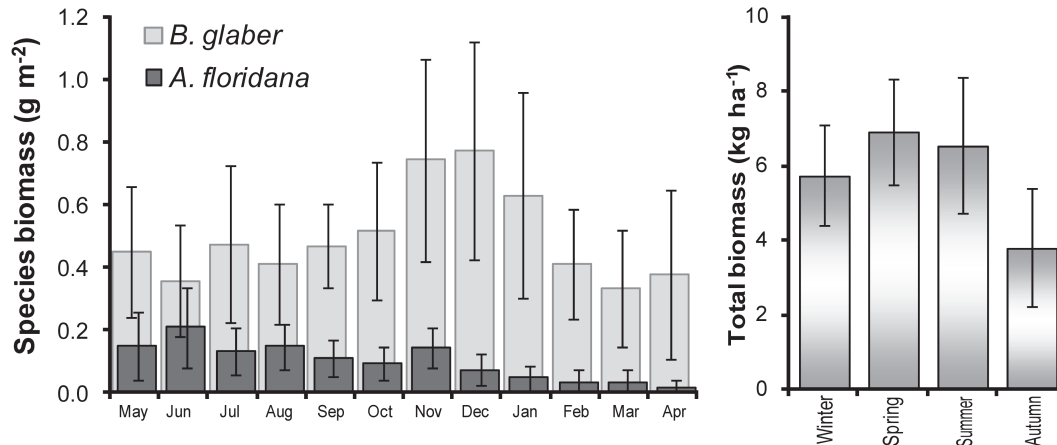| Species	J	Species		B. glaber	A.floridana	Trichorhina sp.	P. tabularis
						L_{AB}	
Trichorhina sp.	5.00	B. glaber			0.25	0.220	0.28
P. tabularis	1.75	A.floridana	S_{AB}	2.32		0.001	0.02
A.floridana	1.37	Trichorhina sp.		6.19	14.15		0.59
B. glaber	0.54	P. tabularis		2.59	6.32	6.550	

Figure 3. Biomass of *A. floridana* and *B. glaber* at Parque Estadual de Itapuã, between May 2004 and April 2005 (on the left) and the summed biomass of the two species per season (on the right). Values are mean ± 95% confidence intervals.

Table III. Measures of species association. In the upper triangle, values are the proportion of individuals occurring together (I_{AB}) and in the bottom triangle there are the coefficient of association, through the mean square contingency (C_{AB}). Both indexes range from -1 (absence of association) to +1 (complete association).

Species		B. glaber	A.floridana	Trichorhina sp.	P. tabularis
				I_{AB}	
B. glaber			0.88	0.07	0.80
A.floridana	C_{AB}	0.22		-0.04	0.63
Trichorhina sp.		0.17	-		0.26
P. tabularis		-	-	0.31	

Table IV. Consumption and egestion rates and assimilation efficiency (%) of *Atlantoscia floridana* and *Balloniscus glaber* feeding on mixed leaf litter from Parque Estadual de Itapuã. All rates refer to dry weight of samples. Values are mean ± 95% confidence intervals.

Feeding rates	A. floridana	B.glaber
Consumption rate (mg mg^{-1} day^{-1})	0.70 ± 0.18	0.34±0.04
Egestion rate (mg mg^{-1} day^{-1})	0.48 ± 0.15	0.25±0.03
Assimilation efficiency (%)	31.00 ± 7.4	27.00±3.50

and the average biomass obtained in the field, we estimate that the population of *B. glaber* could consume 610 kg of leaf litter per ha per year and *A. floridana* population could consume 250 kg ha^{-1} year^{-1}, totaling the processing of 860 kg ha^{-1} year^{-1}, representing 16% of the annual input of leaves. From this amount, 620 kg ha^{-1} year^{-1} would return to the environment as feces.

DISCUSSION

The studied assemblage in PEI was characterized by a high diversity of morphological groups, a high proportion of endemic species and a high density and biomass along the year.

The species *A. itapuensis* and *Trichorhina* sp. presented the common characteristics of the endogean "creeper" species: unpigmented, small and narrow body. The "conglobating" species *P. tabularis* is probably endogean, as it was found in higher numbers within the fine soil layer. It is capable of rolling into a ball, when disturbed, and also to avoid desiccation. The "runner" *A. floridana* has the general morphology of most members of the family Philloscidae – a well pigmented, narrow body possessing long pereiopods adapted to run. Philosciids are common inhabitants of the leaf litter layer. *Balloniscus glaber* is a typical "clinger", as it possesses strong, short pereiopods adapted to grab the substrate, and if disturbed it pretends to be

Table V. Annual litterfall (leaf portion only) of deciduous and semi-deciduous forests of South and Southeast regions of Brazil.

Vegetal community and locality	Annual litterfall kg ha^{-1} year^{-1}	Source
Semi-deciduous (São Paulo, São Paulo)	5900	Meguro et al. (1979)
Semi-deciduous (Jundiaí, São Paulo)	5500	Morellato (1992)
Deciduous (Santa Maria, Rio Grande do Sul)	5100	Cunha et al. (1993)
Semi-deciduous (Campinas, São Paulo)	4500	Martins & Rodrigues (1999)
Semi-deciduous (Ouro Preto, Minas Gerais)	4000	Werneck et al. (2001)
Semi-deciduous (Ouro Preto, Minas Gerais)	5300	Werneck et al. (2001)
Deciduous (Santa Maria, Rio Grande do Sul)	6200	König et al. (2002)

Average 5275 kg ha^{-1} year^{-1}.

dead (thanatosis). It was found in the litter and buried in the upper soil layer. All these groups represent some of the various strategies employed by oniscideans to cope with the enemies and climatic challenges of the terrestrial life (Schmalfuss 1984).

For the coastal plains of Rio Grande do Sul, which includes the PEI area, Lopes et al. (2005) recorded seven oniscidean species. Five of them occur in the present assemblage: *P. tabularis*, *B. glaber*, *A. floridana*, *N. gracilis*, and *Trichorhina* sp. The other two are *B. sellowii* (Brandt, 1833) and *Neotroponiscus daguerrii* (Giambiagi de Calabrese, 1939), and the latter is known to occur in the PEI area (Almerão et al. 2006). *Neotroponiscus daguerrii* is commonly found under tree barks or in bromeliads (Araujo et al. 1996), and therefore was out of our study range. *Balloniscus sellowii* is found near the beaches of PEI, often in abundance but it is not found in the interior of the hill forests.

The present assemblage showed a high number of endemism, which highlights the importance of the PEI area to the conservation of this invertebrate fauna in southern Brazil. Besides *P. tabularis* and *A. floridana*, the other four species are known to occur only in the Rio Grande do Sul state, and to the present *A. itapuensis* is recorded only for the PEI (Araujo & Quadros 2005). Also, the populations of *A. itapuensis* and *N. gracilis* appear to be very small. We should note, however, that their densities could have been underestimated if their true microhabitat was outside the range of our collection method, and this deserves further attention. As the forest ground is the commonest environment studied, nothing is known, for example, about the ecology and biology of endogean and arboricolous oniscidean species.

As expected, the species in PEI were not homogenously distributed. Also, there was a relationship between body size and intraspecific aggregation. It was more intense for the smallest species and less intense for the largest species; moreover, along the year it was more intense during the hottest months. Aggregation can be due to the spatial heterogeneity of resources such as shelters (Hassall & Tuck 2007), mates and good quality food. Isopods are capable of orientate to good quality resources through hygro/tigmokinesis (Edney 1968) and olfaction, by which they perceive the aggregation pheromone present in the feces (Takeda 1984) and air-borne metabolites that indicate

valuable food (Zimmer et al. 1996). Strong intraspecific aggregation may lead to increase interference competition, but it also facilitates coexistence (Presa Abós et al. 2005). The "aggregation model of coexistence" predicts coexistence between potentially competing species where intraspecific aggregation is stronger than interespecific (Presa Abós et al. 2005), which was the case in all species pairs tested in the present study.

It seems that for the oniscideans in PEI, intraspecific aggregation is intense for all species, maybe due to spatial heterogeneity. It is possible that competition is avoided through: 1) abundance of resources, which permits high density/biomass of isopods and/or 2) morphological/ecological differences between species, which allows the exploitation of different resources, or even the same resources in different proportions.

Our results indicate that *A. floridana* and *B. glaber* are the most representative isopods species in the present assemblage, in terms of size (= biomass) and abundance. Their high association indicates similarity in resource use, despite being different in morphology. Also, in the lab they feed intensely on leaf detritus, confirming their detritivorous status. As they are easy to collect and distinguish from the other species, they constitute suitable species for laboratory experiments and were therefore chosen to be our models.

The biomass of the isopod species in PEI was higher than it would be expected for terrestrial isopods, which in forests it is generally below 2000 mg FW m^{-2} (Tsukamoto 1977, Davis & Sutton 1977, Hornung & Warburg 1995, Gongalsky et al. 2005).

The consumption rates obtained for *B. glaber* and *A. floridana* were high, compared to other terrestrial isopods (Zimmer et al. 2002, Dias & Hassall 2005) and detritivorous invertebrates: Diplopods consume up to 51 mg g^{-1} d^{-1} (Szlávecz 1985, David & Gillon 2002). Salt marsh amphipods consume from 7 to 424 mg^{-1} g^{-1} day AFDW, depending on the substrate (Dias & Hassall 2005). Knollenberg et al. (1985) obtained a CR of 11 mg g^{-1} d^{-1} for *Lumbricus terrestris* and Szlávecz (1985) registered a CR of 29 mg g FW^{-1} d^{-1} for *Fridericia ratzeli*, both Oligochaeta species. However, the possibility that the rates presented here for *A. floridana* and *B. glaber* are over estimates cannot be excluded, as we offered mixed litter whereas usually a single species litter is offered as food. Detritivores as isopods and diplopods often show

higher consumption rates when feeding on a mixed litter (SZLÁVECZ & POBOZSNY 1985, ASHWINI & SRIDHAR 2005). Even though, in the context of the present study the use of mixed litter was more appropriated since it better fitted the natural conditions faced by *A. floridana* and *B. glaber* in the field. In the subtropical forests of Rio Grande do Sul, the absence of extremes of climate and the high vegetal diversity of the natural forests (CUNHA 1993) allows a litter production along the entire year (CUNHA 1993, KÖNIG *et al.* 2002) and results in a forest floor with litter from several species and in different stages of decomposition.

The assimilation efficiency of *A. floridana* and *B. glaber* is within the range documented for other onisciddeans (SOMA & SAITÔ 1983). The AE is influenced by the litter type (DUDGEON *et al.* 1990) and its decomposition state (RUSHTON & HASSALL 1983, SOMA & SAITÔ 1983) and varies widely between and within species, notwithstanding it is generally low (less than 30%). This low AE is a product of a nutrient poor diet (decayed litter) which is compensated by increased consumption rates by soil detritivores (DANGERFIELD & MILNER 1996, LAWRENCE & SAMWAYS 2003).

The amount of litter processed by onisciddeans was so far estimated only for a few environments. HASSALL & SUTTON (1977) estimated that *Armadillidium vulgare*, *Porcellio scaber* and *Philoscia muscorum* consumed about 10% of the annual litterfall in grasslands. DIAS & SPRUNG (2003) suggested that *Tylos ponticus* could consume about 10% of the annual primary production of an abundant salt marsh plant. In other two studies, the participation of isopods was lower. MOCQUARD *et al.* (1987) estimated an annual consumption of 210 kg ha^{-1} by *Oniscus asellus* and *Philoscia muscorum*, representing 7% of the annual litterfall and LAM *et al.* (1991) estimated a consumption of only 2.5% of the annual litterfall by four species.

Through high rates of consumption, low efficiency of assimilation and high field biomass, *A. floridana* and *B. glaber* are capable of producing a large amount of fecal pellets, contributing to the soil humus formation, which in turn supplies the forest growth (KNOEPP *et al.* 2000, FÖRSTER *et al.* 2006), as well as other saprophagous fauna. The estimative made in is this study expands the knowledge on isopod's contribution to litter processing and highlights their relevance to the soil conservation in the Neotropical forest studied.

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