Aline Ferreira de Quadros

Ecologia populacional, estratégias reprodutivas e uso de recursos por isópodos terrestres neotropicais (Crustacea, Isopoda)

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Orientador: Profª Drª Paula Beatriz de Araujo

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Tese de doutorado aprovada em ____________

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Profª. Drª. Paula Beatriz de Araujo

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Prof. Dr. Kleber Del-Claro

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Prof. Dr. Sandro Santos

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Profª. Drª. Vera Lúcia da S. Valente Gaiesky

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meios para se atingir um objetivo.
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por me ensinar os bons caminhos.
As respostas ? Essas foram apenas
uma pequena parte desta jornada.
Tu és um exemplo de dedicação e boa vontade.

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Resumo

Os isópodos terrestres (Crustacea, Oniscidea) apresentam adaptações únicas à vida terrestre, tanto fisiológicas quanto morfológicas e comportamentais. Habitam uma grande variedade de ambientes e são facilmente capturados e mantidos em laboratório, constituindo assim um ótimo modelo para investigações que contribuam para um melhor entendimento da ecologia de solo. Apesar de sua grande importância para o funcionamento dos ecossistemas através da detritivoria e da posição chave que ocupam nas teias tróficas, pouco se sabe sobre a ecologia dos oniscídeos Neotropicais. Neste estudo, foram conduzidos estudos comparativos, relativos à ecologia populacional, estratégias reprodutivas e padrões de atividade das duas espécies de isópodos mais abundantes e representativas do sul do Brasil, *Atlantoscia floridana* (van Name, 1940) (Philosciidae) e *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae). Foram comparadas também as preferências alimentares dessas espécies em relação a duas espécies paleárticas, visando propor um modelo para as preferências alimentares dos isópodos. Os estudos relativos à ecologia populacional foram conduzidos no Parque Estadual de Itapuã, no Rio Grande do Sul, Brasil. Após amostragens de maio de 2004 a abril de 2005, 3748 indivíduos foram capturados, correspondendo a seis espécies: *B. glaber*, *A. floridana*, *Pseudodiploexochus tabularis* (Barnard, 1932)(Armadillidae), *Trichorhina* sp. (Platyarthridae), *Alboscia itapuensis* Araujo & Quadros 2005 (Philosciidae) e *Novamundoniscus gracilis* Lopes & Araujo, 2003 (Dubioniscidae). A densidade média foi de 368 ind. m^{-2}. Entre estas espécies, *A. floridana* e *B. glaber* foram as mais abundantes e mostraram alta associação espacial, com 88% dos seus indivíduos ocorrendo juntos e de forma agregada. A biomassa destas duas espécies foi de 4,92 kg ha^{-1} (*B. glaber*) e 0,97 kg ha^{-1} (*A. floridana*). Foi estimado que as duas espécies juntas são capazes de processar 860 kg folhas ha^{-1} ano^{-1}, correspondendo à 16% do aporte anual de folhas na serapilheira. A densidade média de *A. floridana* foi 114 ind. m^{-2} e de *B. glaber* foi 133 ind.m^{-2}. Em relação à ecologia populacional, verificamos diferenças entre as espécies. Enquanto as fêmeas reprodutivas de *A. floridana* estiveram presentes o ano inteiro, *B. glaber* mostrou um período reprodutivo mais curto e restrito ao verão e primavera. As duas espécies mostraram alta abundância de fêmeas reprodutivas e mancas na primavera. As populações responderam de forma diferente à seca observada no verão de 2005. As análises das características de história de vida e das tabelas de vida e fecundidade mostraram que as espécies têm estratégias reprodutivas distintas: *A. floridana* apresenta menor longevidade e desenvolvimento mais rápido, começa a se reproduzir mais cedo, mostra menor investimento parental, maior taxa reprodutiva líquida (R_0), maior taxa de crescimento (*r*) e menor tempo de geração (*T*) em comparação com *B. glaber.* Estas estratégias de história de vida foram interpretadas sob as predições da teoria r-K e relações dessas predições e o grau de especialização de uso de hábitat. O maior tamanho corporal, presença de pulmões pleopodais e comportamento escavador parecem conferir a *B. glaber* uma maior tolerância à dessecação e maior sobrevivência de seus jovens e adultos durante condições climáticas adversas. É proposto que a reprodução contínua, curto tempo de geração e alta proporção de fêmeas reprodutivas são respostas de *A. floridana* à alta mortalidade das suas formas jovens. Em laboratório, o padrão de atividade diário foi investigado em relação à susceptibilidade à dessecação, influência de heterospecíficos no comportamento, frequência das atividades e escolha de hábitat para descanso. Foi verificado que *B. glaber* tem maior atividade durante a noite e *A. floridana* tem um padrão bem variável, o qual não é restrito à fase escura. Devido a essa variabilidade, a sua atividade se sobrepõe à atividade de *B. glaber*, o que leva à rejeição da hipótese de que há partição de tempo entre as espécies. Entretanto, parece haver partição de hábitat através de diferenças dos hábitos de descanso. Observações prévias de que *B. glaber* se enterra no solo durante esse período foram confirmadas. A ausência de interações agressivas entre as duas espécies e a partição de hábitat ajudam a explicar a alta sobreposição espacial e distribuição agregada que as espécies apresentam. As duas espécies mostraram a mesma preferência alimentar, a qual foi também similar à de duas espécies de isópodos paleárticos *Porcellio scaber* Latreille, 1804 (Porcellionidae) e *Philoscia muscorum* (Scopoli, 1763)(Philosciidae). Para concluir, é proposto que isópodos terrestres neotropicais e paleárticos preferem se alimentar de folhas que apresentam uma combinação de altos teores de nitrogênio (>2 %) e cálcio (>1 %) e pouca espessura (<0.1 mm). Muitas propriedades definem os alimentos que são rejeitados, entre elas a presença de tricomas e dureza excessiva (>50 g mm^{-2}). Estes resultados devem auxiliar a formulação de hipóteses sobre as taxas de decomposição e fluxos de energia na presença destes detritívoros.

Palavras-chave isópodos, decomposição, partição de hábitat, teoria r-K, tabelas de vida, atividade circadiana, preferência alimentar

Abstract

Terrestrial isopods (Crustacea, Oniscidea) present unique physiological, behavioral and morphological adaptations to the terrestrial life. They inhabit a large variety of environments and are easily captured and maintained in laboratory, constituting suitable models for studies towards a better understanding of soil ecology. In spite of the key position they occupy in soil food webs as detritivores, almost nothing is known about the ecology of Neotropical species. The present study describes and compares the population ecology, reproductive strategies and activity patterns of the two most abundant and representative species in southern Brazil, *Atlantoscia floridana* (van Name, 1940) (Philosciidae) and *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae). Moreover, their feeding preferences were compared to that of paleartic species aiming the proposal of a template for isopod food choices. All population relates studies were conducted at Parque Estadual de Itapuã, Rio Grande do Sul, southern Brazil. After monthly samplings, from May 2004 to April 2005, 3748 individuals were obtained, comprising six species: *B. glaber*, *A. floridana*, *Pseudodiploexochus tabularis* (Barnard, 1932)(Amadillidae), *Trichorhina* sp. (Platyarthridae), *Alboscia itapuensis* Araujo & Quadros, 2005 (Philosciidae) and *Novamundoniscus gracilis* Lopes & Araujo, 2003 (Dubioniscidae). Total isopod density averaged 368 ind. m^{-2}. Among these species, *A. floridana* and *B. glaber* where the most abundant and showed a high spatial association, with 88% of their individuals occurring together and in an aggregated distribution. Their biomass averaged 4.92 kg ha^{-1} *B. glaber* and 0.97 kg ha^{-1} for *A. floridana*. It was estimated that together they could process 860 kg leaves ha^{-1} year^{-1}, which corresponds to 16% of the annual leaf litter input. Mean density of *A. floridana* was 114 ind. m^{-2} and *B. glaber*'s was 133 ind. m^{-2}. Regarding their population ecology, we found conspicuous differences between species. *Atlantoscia floridana* reproductive females were present throughout the entire year, while *B. glaber* showed a shorter reproduction period, from early spring to early autumn. Both species showed high numbers of reproductive females and mancas during spring. Populations responded differently to the increased dryness observed in the summer of 2005. Analyzes of life history traits and life tables showed contrasting strategies: *A. floridana* showed a shorter lifetime, faster development, earlier reproduction, a smaller parental investment, higher net reproductive rate (R_0), a higher growth rate (r) and a shorter generation time (T) in comparison to *B. glaber*. These life history strategies were interpreted under the predictions of the *r-K* selection theory and the relationship between its predictions and the degree of habitat specialization. The larger body size, presence of pleopodal lungs and the burrowing behavior seems to confer to *B. glaber* a higher tolerance to desiccation and increased young and adult survival under stressful climatic conditions. It is postulated that the continuous reproduction, shorter generation time and higher proportion of reproductive females of *A. floridana* are responses to its high juvenile mortality. Whereas *B. glaber* has a very narrow geographic distribution, *A. floridana* seems to be a successful colonizer, and this success is in part explained by its high reproductive output. These characteristics explain its abundance and commonness. In laboratory, their activity patterns were investigated in relation to differences in susceptibility to desiccation, influence of heterospecifics in behavior, frequency of activities and choice of habitats for resting. *Balloniscus glaber* has a higher activity during the night while *A. floridana* has a highly variable activity pattern, not restricted to the dark phase. Due to this variability, its activity mostly overlaps *B. glaber*'s and thus the possibility of time partitioning was rejected. Instead, habitat partitioning through differences in shelter behavior may contribute to decrease species' niche overlap. Previous observations that *B. glaber* burrows into the soil for resting were confirmed. Both species showed the same preferences when offered a choice of food and preferences rank were also similar to that of paleartic isopods *Porcellio scaber* Latreille, 1804 (Porcellionidae) and *Philoscia muscorum* (Scopoli, 1763) (Philosciidae). To conclude, it is suggested that both paleartic and neotropical species prefer to feed from leaves that have a combination of high amount of nitrogen (>2 %) and calcium (>1 %) and low thickness (<0.1 mm). Many properties define the rejected food types, including trichomes and excessive toughness (> 50 g mm^{-2}). These findings may help formulate predictions about decomposition rates and energy flow in the presence of these detritivores.

Keywords isopods, decomposition, habitat partitioning, r-K theory, life tables, circadian activity, feeding preferences

Apresentação

Ao longo do processo de colonização do ambiente terrestre, os tatuzinhos de jardim desenvolveram variadas e interessantes adaptações à vida nesse novo meio. Esta tese inicia com uma introdução à essas adaptações, com o objetivo de propiciar um melhor entendimento dos padrões populacionais, comportamentais e ecológicos que serão investigados e discutidos com maior detalhe nos capítulos I a V. A seguir, a seção "Material e Métodos" apresenta as espécies que foram objetos deste estudo bem como os locais escolhidos para amostragens. Nesta seção foram incluídas também algumas ilustrações para as informações mencionadas, que embora úteis não puderam ser incluídas nos artigos. Em seguida são apresentados os cinco capítulos, na forma de artigos científicos, que compõem este estudo. O **Capítulo I** caracteriza a diversidade, abundâncias e a distribuição espacial de uma assembléia de isópodos terrestres em uma área de conservação ambiental. Os resultados do Capítulo I ressaltam a importância de *Atlantoscia floridana* e *Balloniscus glaber* no processamento da serapilheira e ciclagem de nutrientes e sua representatividade na fauna de solo, enfatizando suas altas abundâncias e alta associação espacial, e justificam a escolha destas duas espécies como modelos dos estudos seguintes. No **Capítulo II** é abordada a influência dos diferentes graus de adaptação à vida terrestre apresentados por estas espécies na dinâmica de suas populações simpátricas. No **Capítulo III**, os conhecimentos sobre o uso de hábitat pelas espécies são correlacionados com as suas diferentes estratégias de história de vida. No **Capítulo IV**, investiga-se o papel da partição de tempo e microhábitat, em escala circadiana, na coexistência das espécies. No **Capítulo V**, se correlaciona as preferências alimentares com diversos atributos das folhas da serapilheira, e se investiga a generalidade destas relações entre espécies neotropicais e paleárticas. Por fim, as principais conclusões bem como algumas perspectivas de estudos futuros serão apresentadas nas "Considerações Finais".

Introdução geral

Os crustáceos originaram-se nos oceanos, provavelmente no início do período Cambriano (Era Paleozóica; ≈570 mi. a.)(CHEN *et al.* 2001). Neste ambiente houve a grande irradiação de espécies que resultou na diversidade de formas corporais e hábitos de vida observada hoje neste grupo que comporta mais de 167 mil espécies. Somente muito mais tarde na história evolutiva dos crustáceos, no período Terciário (Era Cenozóica), ocorreram as transições que resultaram nas espécies semi-terrestres das ordens Brachyura e Anomura e nas espécies verdadeiramente terrestres das ordens Amphipoda e Isopoda. Os caranguejos braquiúros e anomuros são considerados semi-terrestres pois apesar de realizarem grande parte do seu ciclo de vida em solo, onde alimentam-se e reproduzem-se, necessitam do meio aquático para a dispersão das formas jovens (BLISS 1979).

As ordens Amphipoda e Isopoda pertencem ao táxon Peracarida, o qual agrupa ordens de crustáceos malacostracos que possuem um marsúpio, desenvolvimento direto, e mandíbulas com um processo articulado entre os dentes incisivos e molares (em adultos) denominado *lacinia mobilis* (RICHTER & SCHOLTZ 2001). As reconstruções filogenéticas existentes apresentam propostas contraditórias sobre o parentesco de isópodos e anfípodos. SCHRAM & HOF (1998) os consideram como grupos-irmão, enquanto RICHTER & SCHOLTZ (2001) rejeitam esta condição e separam os anfípodos dos demais grupos de Peracarida que apresentam o estágio de manca (mancóides; Isopoda, Cumacea e Tanaidacea). Independente das suas relações de parentesco, acredita-se que a terrestrialização em ambos grupos se deu gradualmente através das espécies que habitavam a zona supralitoral (EDNEY 1968, HURLEY 1968, FRIEND & RICHARDSON 1986) e aproximadamente na mesma época, visto que seus mais antigos fósseis são encontrados em âmbar e datam do fim do Eoceno e início do Oligoceno (Período Terciário; ≈36 mi.a.). Entretanto, cabe ressaltar que existem dúvidas quanto ao surgimento dos isópodos terrestres pois algumas semelhanças entre espécies africanas e sulamericanas indicam que os isópodos possam ter surgindo no fim do paleozóico, antes da separação destes dois continentes (LITTLE 1984, LEISTIKOW & ARAUJO 2001).

Atualmente, os isópodos terrestres diferem dos anfípodos terrestres em número de espécies, distribuição geográfica e na variedade de ambientes que ocupam. Estas diferenças exemplificam que, sem dúvida, os isópodos terrestres obtiveram muito maior sucesso na exploração do ambiente terrestre em comparação aos anfípodos. Existem cerca de apenas 60 espécies de anfípodos terrestres conhecidas, e todas pertencem à família Talitridae, a qual também contém representantes marinhos e de água doce (HURLEY 1968, FRIEND & RICHARDSON 1986). Os isópodos terrestres distribuem-se globalmente, com exceção do continente antártico, enquanto os anfípodos terrestres têm como distribuição original a região indo-pacífica e algumas poucas espécies ocorrem no hemisfério norte e nas américas apenas por introdução humana (HURLEY 1968, SPICER *et al.* 1987). Em relação aos ambientes que ocupam, os isópodos são encontrados em florestas temperadas e tropicais (ZIMMER 2003, HASSALL *et al.* 2006), cavernas (TUF *et al.* 2008), desertos (LINSENMAIR 1984), montanhas com altitudes de até 3000 m (SFENTHOURAKIS 1992) e campos (HASSALL & SUTTON 1977), enquanto os anfípodos são encontrados em interiores úmidos de florestas próximas à regiões costeiras (FRIEND & RICHARDSON 1986). No Brasil, por exemplo, têm-se o registro de *Talitroides topitotum* (Burt, 1934) em áreas de mata atlântica na costa do país (LOPES & MASUNARI 2004).

1. A subordem ONISCIDEA

A ordem Isopoda constitui um grupo muito diverso entre os Peracarida e é atualmente constituída de cerca de 10.000 espécies (DREYER & WÄGELE 2002), das quais 3.637 são espécies semi-terrestres e terrestres da subordem Oniscidea (SCHMALFUSS 2003). Essa subordem é monofilética e é considerada grupo irmão da subordem Valvifera Latreille, 1802 (ERHARD 1998, DREYER & WÄGELE 2002), sendo dividida nos seguintes táxons (SCHMALFUSS 1989, ERHARD 1998, SCHMIDT 2002, 2003)(Fig. 1):

Subordem Oniscidea Latreille, 1829

Diplocheta Vandel, 1957
  Família LIGIIDAE Brandt & Ratzenburg, 1831 **
Holoverticata
  Tylida
    Família TYLIDAE Milne-Edwards, 1840 *
  Orthogonopoda Tabacaru & Danielopol, 1996
    Microcheta Schmalfuss, 1989
      Família MESONISCIDAE Verhoeff, 1908
    Euoniscoidea Vandel, 1943
      Synocheta Legrand, 1946
        Família SCHOEBLIIDAE Verhoeff, 1938
        Família STYLONISCIDAE Vandel, 1952 *
        Família TITANIDAE Verhoeff, 1938
        Família TRICHONISCIDAE Sars, 1899 *
        Família TURANONISCIDAE Borutzky, 1969
      Crinocheta Legrand, 1946
        Família ACTAECIIDAE Vandel,1952
        Família AGNARIDAE Schmidt, 2003
        Família ALLONISCIDAE Schmidt, 2003
        Família ARMADILLIDAE Brandt & Ratzenburg, 1831 **
        Família ARMADILLIDIIDAE Brandt, 1833 **
        Família BALLONISCIDAE Vandel, 1963 *
        Família BATHYTROPIDAE Vandel, 1952 *
        Família BERYTONISCIDAE Vandel, 1955
        Família BISILVESTRIIDAE Verhoeff, 1938
        Família CYLISTICIDAE Verhoeff, 1949
        Família DELATORREIDAE Verhoeff, 1938
        Família DETONIDAE Budde-Lund, 1906
        Família DUBIONISCIDAE Schultz, 1995 *
        Família EUBELIDAE Budde-Lund, 1899
        Família HALOPHILOSCIDAE Kasselyák, 1930
        Família HEKELIDAE Ferrara, 1977
        Família IRMAOSIDAE Ferrara & Taiti, 1984
        Família OLIBRINIDAE Budde-Lund, 1913
        Família ONISCIDAE Latreille, 1806 **
        Família PHILOSCIIDAE Kinahan, 1857 *
        Família PLATYARTHRIDAE Verhoeff, 1949 *
        Família PORCELLIONIDAE Brandt & Ratzenburg, 1831 **
        Família PUDEONISCIDAE Lemos de Castro, 1973 *
        Família RHYSCOTIDAE Budde-Lund, 1904 *
        Família SCYPHACIDAE Dana, 1852
        Família SCLEROPACTIDAE Verhoeff,1938 *
        Família SPELAEONISCIDAE Vandel, 1948
        Família STENONISCIDAE Budde-Lund, 1904
        Família TENDOSPHAERIDAE Verhoeff, 1930
        Família TRACHELIPODIDAE Strouhal, 1953

* Famílias com registro no Brasil;
** Famílias com registro para o Brasil (espécies exóticas apenas);

O táxon Diplocheta abriga as espécies semi-terrestres dos gêneros *Ligia* Fabricius, 1798 (as "baratinhas da praia") e *Ligidium* Brandt, 1833, os quais compartilham caracteres plesiomórficos com outras subordens de Isopoda (ERHARD 1998), mas atualmente não é considerado monofilético (MICHEL-SALZAT & BOUCHON 2000, MATTERN 2003). Tylida reúne espécies da zona supralitoral dos gêneros *Tylos* Andouin, 1826 e *Helleria* Ebner, 1868. Mesoniscidae abriga apenas duas espécies, *Mesoniscus graniger* (Frivaldsky, 1865) e *Mesoniscus alpicola* (Heller, 1858) (SCHMALLFUSS 2003). O grupo Synocheta abriga espécies higrófilas e em geral de tamanho pequeno. Por fim, Crinocheta abriga a maior parte das espécies de oniscídeos, sendo a mais diversa em formas e hábitos de vida. Grande parte da literatura sobre ecologia populacional, comportamento e fisiologia abrange espécies de Crinocheta, sendo as mais estudadas *Armadillidium vulgare* (Latreille, 1804), *Porcellio scaber* Latreille, 1804, *Oniscus asellus* Linnaeus, 1758 e *Philoscia muscorum* (Scopoli, 1763). Estudos de filogenia molecular indicam que Synocheta e Crinocheta são monofiléticos (MICHEL-SALZAT & BOUCHON 2000, MATTERN 2003) e considerados grupos-irmão (MATTERN 2003). Entre as famílias de Crinocheta, Philosciidae, Dubioniscidae, Platyarthridae, Porcellionidae e Trachelipodidae são consideradas parafiléticas (SCHMIDT 2002, 2003).

2. A colonização do ambiente terrestre pelos isópodos

O cenário evolutivo da colonização do ambiente terrestre compreendeu provavelmente uma gradual transição a partir do ambiente marinho. Considerando que as propriedades físicas são tão diferentes entre os dois ambientes, a transição exigiu mudanças extremas em praticamente todos os aspectos biológicos dos organismos, como a regulação da temperatura, trocas gasosas, percepção, alimentação, locomoção e reprodução (VERMEIJ & DUDLEY 2000). Além disso, as pressões resultantes das interações ecológicas, em particular a competição e predação precisam ser consideradas. Essas duas forças devem ter sido particularmente importantes no caso dos anfípodos e isópodos, pois tendo sido últimos artrópodos a colonizar o ambiente terrestre, encontrariam na fauna de solo muitos representantes de miriápodos, insetos, oligoquetos e aracnídeos (SELDEN 2001), grupos que provavelmente já incluíam predadores e detritívoros.

Como então os isópodos superaram esses desafios? O sucesso do grupo pode ser explicado por um conjunto de pré-adaptações e novidades evolutivas. Inicialmente, os ancestrais marinhos dos oniscídeos já possuíam características corporais que seriam úteis e até mesmo necessárias no novo meio. A locomoção, por exemplo, foi facilitada pela compressão dorso-ventral do corpo e o hábito caminhante, ao invés de nadador ou saltador (EDNEY 1968). Outras pré-adaptações importantes certamente foram a fertilização interna, a qual ocorre na maioria dos Isopoda (WILSON 1991), e o desenvolvimento direto, sem estágios larvais (EDNEY 1968). Entretanto, foram as modificações que ocorreram nas estruturas envolvidas com a reprodução (marsúpio) que possibilitaram a verdadeira independência da água (HOESE 1984). Posteriormente, adaptações fisiológicas e morfológicas permitiram um maior afastamento do litoral e maior tolerância a climas extremos, e ampliaram os limites e paisagens que os oniscídeos puderam ocupar (WIESER 1984). Neste aspecto foram necessárias mudanças em todas as rotas de perda de água passiva, incluindo o tegumento, estruturas respiratórias (SCHMIDT & WÄGELE 2001) e excreção (HARTENSTEIN 1968). Por fim, outras novidades evolutivas permitiram uma maior eficiência na digestão do alimento (e.g. ZIMMER 2006) e reconhecimento e fuga de predadores (e.g. DESLIPPE *et al.* 1995). A seguir serão explicadas em maior detalhe as adaptações para as quais há literatura disponível.

3. Adaptações que permitiram a independência da água

HOESE (1984) considera que, dentre as diversas adaptações para a vida terrestre apresentadas pelos oniscídeos, seu extraordinário sucesso em adquirir a independência da água deve-se principalmente às modificações que se sucederam no marsúpio. Entre os crustáceos, todos os Peracarida incubam seus ovos em uma bolsa (ou microaquário) chamada marsúpio. O marsúpio é formado por oostegitos que são estruturas que se originam das coxas dos pereiópodos (Fig. 2A, B). Supostamente após a fecundação, os ovos deixam os ovários através do oviduto e poro genital (Fig. 2D) e permanecem no marsúpio durante seu desenvolvimento, saindo dele como juvenis ou mancas (Fig. 2E). Nos isópodos aquáticos, os oostegitos têm o formato de placas largas que se sobrepõem formando um assoalho e o marsúpio é aberto nas extremidades ântero-posterior. O movimento dos maxilípodos cria uma corrente ventilatória que permite que a água passe livremente por seu interior, oxigenando os embriões em desenvolvimento (HOESE 1984). O marsúpio do tipo "terrestre" dos oniscídeos não possui estas aberturas nas extremidades e os oostegitos possuem uma cutícula externa espessa e impermeável e formam uma barreira entre o interior úmido do marsúpio e o ambiente externo (HOESE 1984).

Além destas modificações, surgiram nos oniscídeos estruturas únicas entre todos os crustáceos, os cotilédones (Fig. 2C). Os cotilédones surgem nas fêmeas durante o período marsupial e são evaginações dos esternitos constituídas por uma estrutura esponjosa e de cutícula fina, composta por tecido adiposo e hemolinfa (HOESE & JANSSEN 1989). Através deles a fêmea secreta um fluido que nutre e oxigena os filhotes durante todo período intramarsupial (HOESE 1984, SURBIDA & WRIGHT 2001). Podem diferir em número e tamanho entre as espécies, e em uma mesma espécie, o tamanho difere ao longo do desenvolvimento dos filhotes (HOESE 1984). Em *Armadillo officinalis* Duméril, 1816 e *Schizidium tiberianum* Verhoeff, 1923, os cotilédones parecem ter se modificado em sacos que envolvem conjuntos de ovos, dentro do marsúpio (WARBURG & ROSENBERG 1996). LEWIS (1991) e APPEL (2008) demonstraram que os cotilédones variam entre as espécies em número, posição e comprimento, embora o significado destas variações ainda não esteja bem estabelecido (LEWIS 1991). Cabe salientar que, enquanto as fêmeas ovígeras de isópodos aquáticos oferecem apenas uma proteção mecânica aos ovos em desenvolvimento, as fêmeas de oniscídeos protegem a prole da abrasão e dessecação, e ainda provêm oxigênio, água e nutrientes para a prole (HOESE 1984, SURBIDA & WRIGHT 2001).

4. Adaptações para conquista de ambientes mais secos

Diferentemente dos anfípodos terrestres, os oniscídeos não restringiram sua ocupação à ambientes litorâneos ou muito úmidos e colonizaram regiões áridas. No passado, alguns estudos comparativos consideravam os oniscídeos como animais pouco adaptados a ambientes xéricos por serem dependentes de adaptações comportamentais para suportar climas mais extremos (CLOUDSLEY-THOMPSON 1956, EDNEY 1968). Atualmente, considera-se que especialmente os Crinocheta adquiriram uma considerável independência da disponibilidade de água por possuírem muitas adaptações fisiológicas e morfológicas para evitar a dessecação (WRIGHT & O'DONNELL 1995), entre elas: o desenvolvimento do sistema condutor de água (WIESER 1984), a excreção de amônia sob forma gasosa (HARTENSTEIN 1968), a diminuição da permeabilidade da cutícula (HADLEY & QUINLAN 1984, GREENAWAY & WARBURG 1998, NAIR *et al.* 2003), a habilidade de compensar o déficit de água através de um processo ativo (WRIGHT & MACHIN 1993) e o desenvolvimento dos pulmões pleopodais (SCHMIDT & WÄGELE 2001, WRIGHT & TING 2006). Recentemente foi demonstrado que a capacidade volvacional em *Armadillidium vulgare* também contribui para a diminuição da perda de água, provavelmente através da diminuição da taxa metabólica (SMIGEL & GIBBS 2008).

Os oniscídeos são os únicos artrópodos terrestres que possuem excreção amonotélica (HARTENSTEIN 1968). A amônia é conduzida pelo sistema condutor de água ventral e excretada pelos nefrídios maxilares na forma gasosa. A retenção do amonotelia deve ter sido mantida por proporcionar benefícios termodinâmicos aos isópodos, pois além não acarretar em perda de água, há a economia de energia que seria empregada na formação da uréia ou ácido úrico (HARTENSTEIN 1968).

Entre Oniscidea, as espécies variam bastante em sua capacidade de regular a perda de água passiva, e em geral a permeabilidade da cutícula é correlacionada com a disponibilidade de água do ambiente (EDNEY 1968, WHITE & ZAR 1968, GREENAWAY & WARBURG 1998).

Diplocheta e Synocheta apresentam maiores fluxos de água pela cutícula do que Crinocheta (WRIGHT & MACHIN 1990), sendo portanto considerados mais permeáveis. Entre Crinocheta há também bastante variação, sendo as espécies higrófilas mais permeáveis e espécies xéricas como *Venezillo arizonicus* (Mulaik & Mulaik, 1942), *Armadillidium vulgare* e *Armadillo officinalis*, menos permeáveis (GREENAWAY & WARBURG 1998, NAIR *et al.* 2003). Apesar de todas estas evidências, o mecanismo que confere maior impermeabilidade não é bem compreendido, pode ser devido à deposição de lipídios na cutícula e/ou também à uma maior esclerotização do exoesqueleto (HADLEY & QUINLAN 1984).

Outro recurso importante presente nos oniscídeos é a capacidade de explorar o vapor d'água atmosférico através de um processo ativo chamado "*Atmospheric Water Vapor Absorption* (WVA)", que também é realizado por insetos e ácaros (WRIGHT & MACHIN 1990). Estes animais são capazes de absorver água através de uma superfície coletora mantida em contato com o ar úmido e internamente preenchida por um fluido com baixa pressão de vapor de água. A água do ar é termodinamicamente incorporada a este fluido, que precisa então ser movido internamente através de acúmulo de solutos, que ocorre ativamente (WRIGHT & MACHIN 1993). Nos oniscídeos, a absorção ocorre pelos endópodos dos pleópodos e a concentração de solutos ocorre na cavidade entre os exópodos e os esternitos do pleon (WRIGHT & MACHIN 1990). Entre Oniscidea, espécies de Crinocheta dos gêneros *Armadillidium* Brandt, 1833, *Porcellio* Latreille, 1804, *Philoscia* Latreille, 1804, *Porcellionides* Miers, 1877, entre outros, apresentam WVA, assim como *Ligia oceanica* (Linnaeus, 1767)(WRIGHT & MACHIN 1993). Mantendo um influxo de vapor d'água altamente eficiente, esses isópodos podem compensar a perda de água via transpiração e tolerar ambientes xéricos por um maior período de tempo.

O tamanho relativamente pequeno dos artrópodos, que resulta em uma alta relação superfície/volume e a maior pressão de oxigênio no ar, em comparação com a água, facilitam a difusão de oxigênio através do tegumento (SELDEN 2001). À medida em que os oniscídeos afastaram-se de ambientes saturados de umidade aumentou a necessidade de proteger o tegumento contra a dessecação, tornando-os menos permeáveis. Ao mesmo tempo, a diminuição da permeabilidade reduziu a capacidade de obtenção de oxigênio por difusão através do tegumento e assim foram necessárias estruturas respiratórias cada vez mais especializadas em obter oxigênio sem expor grandes superfícies à dessecação (WRIGHT & TING 2006).

As estruturas respiratórias dos oniscídeos passaram por uma conspícua diferenciação durante a evolução do grupo e tornaram-se um importante caráter na sua classificação (SCHMIDT & WÄGELE 2001). Nos isópodos aquáticos de modo geral, as trocas gasosas ocorrem na face dorsal dos exópodos dos pleópodos, onde estão localizadas as brânquias (CAREFOOT & TAYLOR 1995). Nos isópodos semi-terrestres do gênero *Ligia* observa-se que a superfície respiratória localiza-se na face ventral, a qual fica então em maior contato com o ar, em comparação com a dorsal onde a circulação de ar é bem reduzida (CAREFOOT & TAYLOR 1995, SCHMIDT & WÄGELE 2001). SCHMIDT & WÄGELE (2001) enfatizam que a mudança da superfície respiratória da face dorsal para a face ventral foi o primeiro importante passo em direção ao sucesso em áreas de menor umidade. A partir deste plano básico, três padrões de diferenciação das estruturas respiratórias podem ser identificadas nos demais oniscídeos. Entre Tylida houve um aumento nos dobramentos da cutícula ventral, originando pulmões internos com espiráculos ventrais (SCHMIDT & WÄGELE 2001). Synocheta e Mesoniscidae adquiriram um hábito endógeo ou cavernícola (SCHMALFUSS 1984) e constituem espécies de pequeno tamanho corporal que vivem em ambientes saturados de umidade. Estes grupos mantiveram o mesmo padrão encontrado em Ligiidae (SCHMIDT & WÄGELE 2001) e também mantiveram as trocas gasosas via tegumento. Já entre Crinocheta pode ser observado um gradiente de modificações, desde os tipos mais basais - as superfícies respiratórias ventrais - até pulmões pleopodais internos dotados inclusive de espiráculos como mecanismo de fechamento. Em algumas espécies de Crinocheta (*Alloniscus* spp., *Philoscia* spp., *Oniscus* spp.) a superfície respiratória voltou a se localizar na face dorsal, visando agora a proteção contra dessecação (área respiratória dorsal, ou "*Oniscus*-type lung") (SCHMIDT & WÄGELE 2001). Em outros grupos (*Armadillidium* spp., *Porcellio* spp., *Trachelipus* spp.), muitos dobramentos na superfície dorsal criaram túbulos de ar que são parcialmente cobertos por um prolongamento da cutícula (pulmões parcialmente cobertos, ou "*Trachelipus*-type lung") (SCHMIDT & WÄGELE 2001). O próximo passo, encontrado em espécies de ambientes xéricos como *Armadillo* spp. e *Hemilepistus* spp. e espécies de Eubelidae (FERRARA *et al.* 1991), foi o desenvolvimento de um pulmão totalmente fechado, que consiste de túbulos de ar internos que abrem através de um ou mais espiráculos ("*Hemilepistus*-type lung") (SCHMIDT & WÄGELE 2001). Por fim, a organização mais complexa é encontrada em espécies do deserto gênero *Periscyphis* (FERRARA *et al.* 1991). Neste tipo de pulmão, o espiráculo situa-se muito próximo à área de inserção dos pleópodos e a área perispiracular é bem reduzida. As ramificações tubiformes internas estendem-se além dos exópodos e penetram na cavidade corporal ("*Periscyphis*-type lung") e oxigenam a hemolinfa nos exópodos e também no interior do corpo (FERRARA *et al.* 1991).

5. Outras novidades evolutivas em Oniscidea

Além dos pulmões pleopodais e da presença dos cotilédones no marsúpio, explicadas anteriormente, os oniscídeos apresentam outras características biológicas únicas, relacionadas com os novos recursos encontrados pelos isópodos nos ambientes terrestres, como alimento derivado de plantas terrestres (e.g. ZIMMER 2006) e novos predadores (e.g. DESLIPPE *et al.* 1995).

As fontes de alimento de animais detritívoros diferem consideravelmente entre os meios aquático (marinho ou doce) e terrestre. As plantas terrestres têm maior quantidade de lignina e celulose e compostos secundários, e menores teores de nutrientes, caracterizando assim um alimento pobre em nutrientes e de difícil manipulação, pois muitas enzimas são necessárias para a quebra de compostos complexos (ZIMMER 2002, ZIMMER 2008). Durante a colonização do ambiente terrestre ocorreram adaptações fisiológicas para aumentar a eficiência da digestão dessas novas fontes de alimento, mas provavelmente a aquisição de bactérias endossimbiontes do hepatopâncreas constituiu um grande avanço (ZIMMER 2006). Estas bactérias contribuem para a digestão da celulose e lignina, fornecendo enzimas consideradas "funcionalmente endógenas" (ZIMMER & TOPP 1998, ZIMMER *et al.* 2001). Estudos recentes indicam que a subordem Oniscidea foi colonizada pelas mesmas linhagens de bactérias hepatopancreáticas, e em Crinocheta são encontradas duas linhagens distintas, '*Candidatus* Hepatoplasma crinochetorum' (Mollicutes) e '*Candidatus* Hepatincola porcellionum' (Rickettsiales) (WANG *et al.* 2007). Representantes marinhos das subordens Sphaeromatidea e Valvifera não possuem qualquer tipo de endosimbiontes no hepatopâncreas (ZIMMER *et al.* 2001).

Sendo detritívoros, os isópodos terrestres atuam como elementos de ligação entre os produtores primários e os níveis tróficos mais altos. Seus predadores conhecidos incluem artrópodos, como quilópodos, coleópteros (larvas e adultos), larvas de Neuroptera, aranhas, pseudoescorpiões e opiliões, além de vertebrados tais como aves, anfíbios da família Leptodactilydae e répteis das famílias Gekkonidae e Scincidae (SUNDERLAND & SUTTON 1980, VITT *et al.* 2000, VAN SLUYS 2001, SANTOS & GNASPINI 2002). Para se proteger contra predadores os isópodos podem apresentar defesas morfológicas, como presença de projeções e forte calcificação do exoesqueleto; comportamentais, como a tanatose e capacidade volvacional (SCHMALFUSS 1984) e químicas, como a secreção de uma substância adesiva, não-tóxica, que retarda predadores de menor porte, tais como artrópodos (DESLIPPE *et al.* 1995). Conforme destacado por GORVETT (1952) esta secreção é produzida por glândulas localizadas nos urópodos, as quais estão presentes apenas em Oniscidea, e representam portanto uma adaptação à terrestrialização. DESLIPPE *et al.* (1995) demonstraram que a secreção da substância adesiva por essas glândulas é um eficiente método para evitar predação de *O. asellus* por *Formica exsectoides* Forel, 1886 (Formicidae). A substância não é tóxica às formigas, e atua como um mecanismo de fuga, pois as formigas, ou outros artrópodos, ficam presos na substância por alguns segundos. Por ser de natureza protéica, a produção desta substância acarreta um alto custo energético para os isópodos (GORVETT 1952).

6. Os grupos eco-morfológicos

Em ecologia, grupos funcionais são agrupamentos de organismos independentes de suas relações filogenéticas, baseadas na morfologia, fisiologia, comportamento e/ou posição trófica. Em Oniscidea, a única proposta de classificação em grupos funcionais é a de SCHMALFUSS (1984), o qual reconhece seis grupos baseados na morfologia e estratégia anti-predatória (Fig. 3):

"***Runners***" (Fig. 3A) – são isópodos com corpo alongado e pereiópodos fortes e relativamente bem longos, adaptados para fuga rápida quando sob ameaça; esta estratégia é geralmente apresentada pelos representantes da família Philosciidae e representa o plano corporal básico dos oniscídeos, visto que corresponde ao padrão de *Ligia* spp. Geralmente apresentam também antenas longas (SCHMALFUSS 1998).

"***Clingers***" (Fig. 3B) – são animais com os tergitos achatados e largos, que quando perturbados, agarram-se firmemente ao substrato e permanecem imóveis, imitando um animal morto; espécies dos gêneros *Balloniscus* Budde-Lund, 1908, *Trachelipus* Budde-Lund, 1908 e *Porcellio* representam esta categoria;

"***Rollers***" (Fig. 3C) – quando ameaçados, os indivíduos encolhem-se formando uma bola, de maneira a expor seu rígido exoesqueleto e impedir o acesso às suas partes ventrais vulneráveis. Esta conformação é possível através de modificações dos tergitos, que são semicirculares. Ocorrem nas famílias Armadillidae, Armadillidiidae, Eubelidae e Tylidae.

"***Spiny forms***" – são encontradas apenas em regiões tropicais. Caracterizam-se por possuírem protuberâncias conspícuas nos tergitos, que protegem contra predação.

Todos os representantes conhecidos têm também capacidade volvacional. Alguns representantes são encontrados nas famílias Eubellidae e Armadillidae;

"*Creepers*" (Fig. 3D) – espécies pequenas (menores que 5 mm comprimento) com pereiópodos relativamente curtos e fracos. Estas espécies são adaptadas para ambientes rochosos e interiores de cavernas com interstício estreito e substrato permanentemente úmido. Muitas espécies não possuem olhos ou pigmentação no exoesqueleto. Assim como os *rollers*, apresentam antenas mais reduzidas (SCHMALFUSS 1998).

"*Non-conformists*" (Fig. 3E) – como o nome da categoria diz, representa as espécies com adaptações únicas entre os Oniscidea e que não se encaixam nas descrições acima. São exemplos *Platyrathrus hoffmannseggi* Brandt, 1833 e *Platyrathrus schoblii* Budde-Lund, 1885, espécies comensais de ninhos de formigas e cupins (HORNUNG *et al.* 2005) e *Hemilepistus reaumurii* (Milne-Edwards, 1840), espécie do deserto que escava e habita tocas subterrâneas (LINSENMAIR 1984).

Recentemente, HASSALL *et al.* (2006) estudando a fauna de oniscídeos da Malásia, descrevem um sétimo grupo, o dos "*jumpers*" após terem capturado uma espécie nova para a ciência do gênero *Burmoniscus* Collinge, 1914. Segundo os autores, a espécie é capaz de saltar mais de 20 cm de altura (HASSALL *et al.* 2006).

Embora muito útil, as características ecológicas dos oníscídeos, bem como suas respostas comportamentais à estímulos abióticos e bióticos raramente são discutidos em relação à classificação em grupos morfológicos. Pode-se citar MA *et al.* (1991), que compararam as estratégias de vida de "runners" e "rollers" e HASSALL & TUCK (2007), que compararam o comportamento de uso de abrigos por "runners", "rollers" e "creepers".

Objetivos

Esta tese teve como objetivos principais contribuir para o conhecimento da ecologia dos oniscídeos neotropicais, utilizando como modelos duas espécies simpátricas, *Atlantoscia floridana* (van Name, 1940) e *Balloniscus glaber* Araujo & Zardo, 1995, investigando seus padrões populacionais, comportamentais e nutricionais.

Capítulo I. Assembléia de isópodos de Itapuã

A. Caracterizar a fauna de isópodos terrestres de solo e serapilheira em uma área de floresta do Parque Estadual de Itapuã, RS, observando suas abundâncias, intensidade de agregação e padrão de co-ocorrência das espécies;

B. Caracterizar a importância de *A. floridana* e *B. glaber* para o processamento de serapilheira, obtendo em laboratório as taxas de consumo e egestão da mesma e relacionando esta informação com o aporte médio anual estimado na literatura;

Capítulo II. Ecologia populacional

C. Conhecer o período da reprodução, densidades mensais populacional, bem como das mancas e fêmeas ovígeras, relacionando-os com fatores abióticos (temperatura, precipitação, conteúdo de água do solo;

D. Caracterizar a estrutura populacional, considerando idade e tamanho, das duas espécies;

Capítulo III. Estratégias reprodutivas

E. Elaborar as tabelas de vida e fecundidade das duas espécies, obtendo o tempo de geração, taxa reprodutiva líquida e taxa de crescimento *per capita*;

F. Caracterizar as estratégias reprodutivas de *A. floridana* e *B. glaber*, utilizando as predições da teoria “*r-k*”;

Capítulo IV. Atividade circadiana

G. Caracterizar os padrões de atividade circadianos, observando os ciclos de atividade e descanso, uso de hábitat e a interação entre as espécies;

Capítulo V. Preferência alimentar

H. Caracterizar a serapilheira de uma área de floresta semidecidual neotropical;

I. Caracterizar as cinco espécies vegetais mais abundantes através da espessura, dureza, e conteúdos foliares de: fenóis, lignina, celulose, carbono, nitrogênio, cálcio e fósforo;

J. Realizar testes de preferência alimentar e performance considerando plantas e isópodos neotropicais e paleárticos;

L. Elaborar um modelo para as preferências alimentares dos isópodos terrestres, levando em consideração diferenças entre neotropicais e paleárticos.

Material e métodos

Nesta seção são apresentadas com maior detalhe as espécies utilizadas como modelo de estudo bem como as áreas onde foram conduzidos o trabalho de campo e os demais experimentos. Os demais procedimentos, experimentos e análises estatísticas utilizadas são descritos em detalhes nos seus respectivos capítulos.

1. Os modelos de estudo

As espécies estudadas foram *Atlantoscia floridana* (van Name, 1940) (Philosciidae) e *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae), ambas famílias do grupo Crinocheta. Entre Crinocheta, Philoscidae constitui um grupo de cerca de 450 espécies e uma centena de gêneros, caracterizadas em geral pelo corpo alongado e de superfície lisa, flagelo das antenas com três artículos (caráteres plesiomórficos) e pleon mais estreito que o pereion (LEISTIKOW 2001, SCHMIDT 2003). Entretanto, estudos taxonômicos e filogenéticos têm evidenciado que a família Philosciidae não constitui um grupo monofilético (SCHMIDT & LEISTIKOW 2005). A família Balloniscidae foi criada para agrupar os gêneros *Plataoniscus* Vandel, 1963 e *Balloniscus* Budde-Lund, 1908 devido à presença de cinco pares de pulmões pleopodais (LEISTIKOW 2001). *Balloniscus* havia sido instituído inicialmente como subgênero de Philosciidae, para abrigar algumas espécies do gênero *Philoscia* Brandt, 1833 (SCHMIDT & LEISTIKOW 2004). ARAUJO & LEISTIKOW (1999) designaram *Philoscia sellowii* como a espécie tipo de *Balloniscus*, considerando-o como um gênero da família Philosciidae, mas LEISTIKOW (2001) transferiu-o novamente para a família Balloniscidae.

Atualmente, o gênero *Atlantoscia* está representado por três espécies, as quais ocorrem no Brasil: *A. floridana*, *A. rubromarginata* Araujo & Leistikow, 1999 e *Atlantoscia* sp.

n., a qual encontra-se em processo de descrição (PB Araujo, comunicação pessoal). O gênero *Balloniscus* é formado por seis espécies válidas: *B. brevicornis* (Budde-Lund, 1885), *B. maculatus* (Budde-Lund, 1885), *B. nigricans* (Budde-Lund, 1885), *B. paraguayanus* (van Name, 1936), *B. sellowii* (Brandt, 1833) e *B. glaber* (SCHMALLFUSS 2003), sendo apenas *B. sellowii* e *B. glaber* registradas para o Brasil (ARAUJO *et al.* 1996).

Atlantoscia floridana (van Name, 1940) (Fig. 4A, D)

Sinonímia: *Philoscia floridana* van Name, 1940
Chaetophiloscia paulensis Moreira, 1927
Ocelloscia floridana comb. n. Schultz & Johnson, 1984
Atlantoscia alceui Ferrara & Taiti, 1981

Descrição (segundo ARAUJO & LEISTIKOW 1999):

Coloração. Manchas brancas no cefalotórax, pereion e pleon indicando as inserções musculares na cutícula. Ventralmente é pálida sem marcações características. **Cefalotórax.** Linha frontal ausente, lobos laterais slight, linha supra-antenal presente, olhos compostos por até 20 omatídeos. **Pereion.** Tegumento liso com alguns tubérculos pequenos com setas tricornes esparsas, placas coxais com sulco marginal, poucos (1-3) poros glandulares e nódulos laterais, inseridos dorsalmente na placa coxal IV, margem caudal das placas coxais com linha de distintas escamas quadrangulares. **Pleon.** Mais estreito que o pereion, com pequenas neuropleuras nos segmentos 3 a 5, pleotelso com margens laterais côncavas e com setas tricornes. **Antênula.** Tri-articulada com artículo distal coniforme, na metade do comprimento da antênula apresenta 5 pares de estetascos na margen medial até o ápice. **Antena.** Flagelo composto por três artículos, praticamente subiguais em comprimento, o artículo distal com órgao apical na metade do comprimento da articulação distal, sensilas livres tão longas quanto às lamelas cuticulares, artículos pedunculares cobertos por setas tricornes. **Mandíbula.** Penicílio molar consistindo de 5 ramificações fusionadas na base, setas plumosas adicionais proximais. **Maxílula.** Endito lateral com 4+6 dentes, um tripartido, endito medial com dois penicílios fracos e sem ponto apical. **Maxila.** Lobo medial menor que a metade da largura do lobo lateral, densamente coberto com finas setas triquiformes, lobo lateral esparsamente coberto por escamas pectinadas. **Maxilípodo.** Base com sulco lateral latero-proximal e com escamas cuticulares, palpo com conjunto interno de setas consistindo de setas longas e curtas, tufo medial com 4 setas, seta do artículo proximal forte. **Pereiópodos.** Alongados, contendo muitos setas tricornes, carpo I com pincel limpeza da antena, espinhos sensoriais ornamentais com ápice duplo, dáctilo com seta interungual levemente mais curta. **Pleópodos.** Exópodos retangulares obliquamente com ponto distinto, margem lateral com 2 a 3 espinhos sensoriais, exópodo do P5 com linha transversa de escamas longitudinais na superfície caudal, endópodos com margem lateral sinuosa inconspícua, pequenas áreas respiratórias retroproximais no lado caudal dos exópodos. **Urópodos.** Exópodo com inserção distal do endópodo, protopodito com sulco lateral. **Papila genital.** Escudo ventral levemente mais curto que a papila, orifícios na margem apical truncada transversalmente.

Atlantoscia floridana destaca-se por sua ampla distribuição geográfica e variedade de ambientes que ocupa (Fig. 5). LEMOS DE CASTRO (1985) registra sua ocorrência em todos estados costeiros brasileiros. Na região sul do Brasil, ARAUJO *et al.* (1996) registram sua ocorrência em áreas naturais e urbanas, como florestas, campos, jardins e pátios de residências. Quanto aos grupos ecomorfológicos, *A. floridana* é considerada um "runner".

Atlantoscia floridana foi a primeira espécie neotropical a ser estudada quanto à sua biologia e ecologia. ARAUJO & LEISTIKOW (1999) forneceram uma re-descrição da espécie. LEISTIKOW & ARAUJO (2001) apresentam detalhes das suas estruturas respiratórias. Segundo os autores, *A. floridana* apresenta apenas uma área respiratória, com a cutícula distal ao átrio mais fina mas sem dobramentos e este representa o estado mais primitivo dos pulmões pleopodais. AMATO *et al.* (2003) registraram a ocorrência de distrofia pigmentar nessa espécie, em indivíduos parasitados por uma espécie de *Centrorhynchus* Lühe, 1911 (Acanthocephala) (Fig. 4D). ARAUJO *et al.* (2004b) descrevem a duração e modificações morfológicas que ocorrem nos estágios de manca (I, II e III). ARAUJO & BOND-BUCKUP (2004) fornecem as curvas de crescimento baseadas no modelo de crescimento de von Bertallanfy. Nesse estudo os autores demonstraram uma expectativa de vida diferencial para machos e fêmeas, sendo um ano e meio e dois anos e quatro meses, respectivamente. ARAUJO *et al.* (2004a) descrevem o surgimento dos caracteres sexuais secundários. Após os três estágios de manca, machos passam por três estágios juvenis, e as fêmeas por seis. A idade da maturação sexual estimada é de 1.5 meses para machos e 3 meses para fêmeas (ARAUJO *et al.* 2004a). ARAUJO & BOND-BUCKUP (2005) estudaram a ecologia populacional da espécie em uma mata de restinga da Reserva Biológica do Lami, uma área de conservação de Porto Alegre. Essa população foi caracterizada por altas densidades (até 1040 ind. m^{-2}) bem como grandes flutuações na mesma ao longo das estações. Ainda, os autores demonstram que há sobreposição de gerações, sendo difícil a separação das coortes, e concluem que a espécie é iterópara. Em todos os meses são encontradas fêmeas ovígeras e mancas (ARAUJO & BOND-BUCKUP 2005).

Balloniscus glaber Araujo & Zardo, 1995 (Fig. 4B)

Descrição (segundo ARAUJO & ZARDO 1995):

Coloração. Padrões diversificados, pigmentação variando de castanho escuro a claro, às vezes avermelhada ou acinzentada, variegada em maior ou menor intensidade com manchas amarelas; faixa mediana dorsal longitudinal escurecida, freqüentemente com manchas claras desde o pereionito I até o final do pleon; geralmente com faixa longitudinal escurecida na borda dos pereionitos; antenas de cor castanha uniforme. **Cefalotórax**. Cabeça pouco envolvida pelo pereionito I; linha frontal presente delimitando os lobos laterais pouco acentuados em frente aos olhos; linha supra-antenal sinuosa; olhos com 20-22 omatídeos. **Pereion**. Superfície lisa, brilhante com tricornes curtos e pouco numerosos; nódulos laterais do pereionito VII deslocados da extremidade para dentro; cerca de 15 poros grandulares na borda dos pereionitos; epímeros dos pereionitos V, VI e VII projetados para trás com ponta aguda; pereiópodos com cerdas, espinhos. **Pleon.** Estreitando-se gradualmente. **Telso.** Triangular com ápice agudo, ultrapassando a extremidade distal do protopodito dos urópodos. **Antênula**. Artículo distal com cerca de 12 estetascos, sendo dois apicais. **Antena**. Quando estendida para trás alcança o pereionito II; flagelo do mesmo tamanho que o artículo IV do pedúnculo. **Maxílula**. Exito com 4 + 6 dentes (quatro fendidos). **Maxilípodo**. Endito quadrangular armado de um dentículo sobreposto a outro na borda distal interna e outro na borda superior externa. **Urópodos**. Exópodos cerca de 1,5 vezes mais longos que o telso; endópodos com metade do comprimento dos exópodos. **Dimorfismo sexual**. Macho com pereiópodo I com mero e carpo providos de numerosas cerdas; pereiópodo VII sem dimorfismo aparente; pleópodo I com exópodo quadrangular e linha marginal distal reta e endópodo alongado, provido de pelos e de uma série de pequenas cerdas na extremidade distal; pleópodo II com exópodo subtriangular e endópodo com a extremidade distal rombuda.

O conhecimento sobre *Balloniscus glaber* é ainda incipiente e na ocasião do início deste estudo, em 2004, consistia apenas da descrição original da espécie e registros de ocorrência no Rio Grande do Sul (ARAUJO & ZARDO 1995, ARAUJO *et al.* 1996). Por se tratar de uma espécie com distribuição geográfica muito restrita (Fig. 6), BOND-BUCKUP *et al.* (2003) incluíram *B. glaber* no Livro Vermelho da Fauna Ameaçada do RS. Ao longo dos últimos anos alguns estudos foram realizados e nos permitiram conhecer um pouco mais sobre a distribuição e biologia dessa espécie no Rio Grande do Sul. LOPES *et al.* (2005) compararam a fauna de oniscídeos da planície costeira, encosta da Serra Geral e planalto Rio-Grandense, e mencionam que *B. glaber*, juntamente com *A. floridana* ocorreram nos três ambientes e em alta abundância relativa, correspondendo juntos à 72% do total de espécimes capturados. No Parque Estadual de Itapuã, também no RS, ALMERÃO *et al.* (2006) inventariaram a fauna de oniscídeos da Praia de Fora e da Trilha Pombas-Onça e registraram a ocorrência de *B.*

glaber nas áreas de floresta dos morros do Parque. MEINHARDT *et al.* (2007) estudaram o seu crescimento, com base na estrutura de tamanho de uma população do Parque de Itapuã. Em seu estudo, verificaram que machos e fêmeas apresentam crescimento diferencial, sendo que as fêmeas atingem um maior tamanho corporal e têm maior longevidade, mas apresentam uma taxa de crescimento menor que os machos (MEINHARDT *et al.* 2007). Recentemente, populações de *B. glaber* e *Balloniscus sellowii* (Brandt, 1933) da planície costeira do RS têm sido estudadas quanto à sua estruturação genética com base no ADN mitocondrial e ainda, quanto a diversidade dos endossimbiontes *Wolbachia* (M.P. ALMERÃO, comunicação pessoal).

Balloniscus glaber pertence ao grupo ecomorfológico dos "clingers". Essa espécie diferencia-se de *A. floridana* e dos demais oniscídeos da fauna conhecida do RS, por apresentar características ecológicas bem peculiares (Fig. 7). ARAUJO & ZARDO (1995) na descrição original da espécie comentam que *B. glaber* realiza tanatose e também são freqüentemente encontrados enterrados. Ao serem perturbados, os indivíduos reagem encolhendo os pereiópodos e arqueando o corpo, parecendo uma vírgula, e podem permanecer nessa posição por vários minutos (Fig. 7B). A habilidade escavatória é facilmente observada se os animais são deixados em ambientes com uma camada de terra (Fig. 7D, E). Adicionalmente, seus indivíduos apresentam um grande polimorfismo de cor, sendo as mancas despigmentadas e juvenis e adultos apresentando padrões marrom claro e escuro, amarelo claro e escuro, cinza e vermelho escuro (Fig. 7A). Ao longo deste estudo, vários indivíduos de *B. glaber*, de diversas populações, foram encontrados sendo parasitados por espécimes de Acanthocephala, embora nenhum mostrando distrofia pigmentar (Fig. 7C), indicando que assim como *A. floridana*, esta espécie também participa do ciclo desses parasitos.

2. Populações estudadas

Os indivíduos utilizados neste estudo foram provenientes de duas áreas diferentes. Para realizar os estudos que envolveram coletas mensais ao longo de um ano (capítulos I, II e III), desejava-se uma área natural e com a menor influência antrópica possível. Para tanto, foi escolhida uma área do Parque Estadual de Itapuã (Viamão, RS) destinada à conservação e não acessível ao público em geral (Fig. 8A, ao sul). Já para os experimentos de laboratório dos capítulos IV e V, foi escolhida uma área junto ao Campus da UFRGS (Porto alegre, RS), de fácil acesso e que se mostrou uma fonte abundante de *A. floridana* e *B. glaber* (Fig. 8A, ao norte).

A região de Porto Alegre onde estão localizadas as áreas de estudo é considerada um ecótono entre formações vegetais pioneiras de influência marinha e florestas estacionais semideciduais (LEITE & KLEIN 1990). Distantes cerca de 50 km, as duas áreas de estudo fazem parte dos cordões de morros graníticos que formam a projeção mais setentrional do Escudo Rio-Grandense (MENEGAT *et al.* 1998) e possuíam originalmente as mesmas formações vegetais. As áreas naturais desses morros são caracterizadas por campos e florestas entremeados por seixos e afloramentos graníticos. Os campos são relictos da época de clima glacial, seco e frio e anterior às florestas atuais (PORTO 1998). As florestas que ocupam os morros são estacionais semideciduais, do tipo higrófilas e mesófilas, nas quais grande parte das espécies vegetais tem características tropicais, com provável origem na Floresta Ombrófila Densa (Mata Atlântica) (BRACK *et al.* 1998). O clima dessa região é temperado, sem estação seca e com verões quentes (tipo CFa; subtropical úmido, de acordo com a classificação de Köppen)(PEEL *et al.* 2007). A pluviosidade média anual é de 1.300 mm, com chuvas bem distribuídas ao longo do ano (RIO GRANDE DO SUL 1997).

O Parque Estadual de Itapuã é uma unidade de conservação estadual que compreende uma área de 5.556 ha localizada ao sul do distrito de Itapuã, no município de Viamão, RS (Fig. 8B). Situa-se entre as coordenadas 50° 50' e 51° 05' W e 30° 20' e 30 27' S, distante 57 km do centro de Porto Alegre. Na área do Parque observa-se um mosaico de paisagens, como morros graníticos cobertos por florestas semideciduais, campos, dunas e vegetação de restinga nas margens das lagoas e Lago Guaíba (Fig. 8C). Essa diversidade deve-se à coexistência de duas províncias geomorfológicas: o Escudo Rio-Grandense, representado pelas coxilhas e morros graníticos e a Planície Costeira, representada por extensas superfícies planas ou levemente onduladas. Grande extensão dos limites do Parque é banhada pelo Lago Guaíba e pela Laguna dos Patos, que fazem parte da Bacia Hidrográfica do Guaíba e grande parte da área do parque é ocupada pela Lagoa Negra. O zoneamento do Parque instituiu três zonas de uso: zonas de uso intensivo, abertas à visitação geral do público; zonas de uso extensivo, utilizadas ocasionalmente por visitantes com a presença de guias; e a zona primitiva, destinada à preservação e pesquisa científica (RIO GRANDE DO SUL 1997). No Parque foi escolhida uma área de floresta em encosta de morro, adjacente à Trilha da Onça, a qual não é utilizada para visitação. Nessa área ALMERÃO *et al.* (2006) verificaram a coexistência de seis espécies de oniscídeos, incluindo *A. floridana* e *B. glaber*. A Trilha da Onça inicia no extremo esquerdo da Praia das Pombas (aberta à visitação do público) e percorre 4 km até a Praia da Onça (Fig. 8D, E). Esta trilha pertence à Zona de Uso Extensivo, que é constituída em sua maior parte por áreas naturais e representa a transição entre a Zona de Uso Intensivo (neste caso, a Praia das Pombas) e a Zona Primitiva.

O Morro Santana localiza-se na divisa dos municípios de Porto Alegre e Viamão (Fig. 9A). Totaliza uma área de 1459 ha, dos quais 660 ha pertencem à UFRGS. Atualmente, planeja-se implantar nessa área uma unidade de conservação de 360 ha. As florestas ocupam cerca de 30% da área, áreas urbanas 29.7% e campos, 15% (BORTOLOTTI 2006). Nas áreas não-urbanas do Morro, BORTOLOTTI (2006) reconhece três tipos fitofisionômicos de florestas, correspondendo a áreas em estágio sucessional inicial até áreas em estágio de regeneração bem avançados. A área escolhida para estudo no Morro tem cerca de 1 ha e fica próxima ao Departamento de Ecologia da UFRGS. Essa área encontra-se em estágio intermediário a avançado de regeneração (Fig. 9B) e na serapilheira ocorrem em simpatria as espécies *A. floridana* e *B. glaber*, além de *Novamundoniscus gracilis* Lopes & Araujo, 2003, *Styloniscus* sp. e *Trichorhina* sp. (obs. pessoal). A lista das espécies arbóreas e arbustivas encontradas nesse fragmento está incluída no capítulo V.

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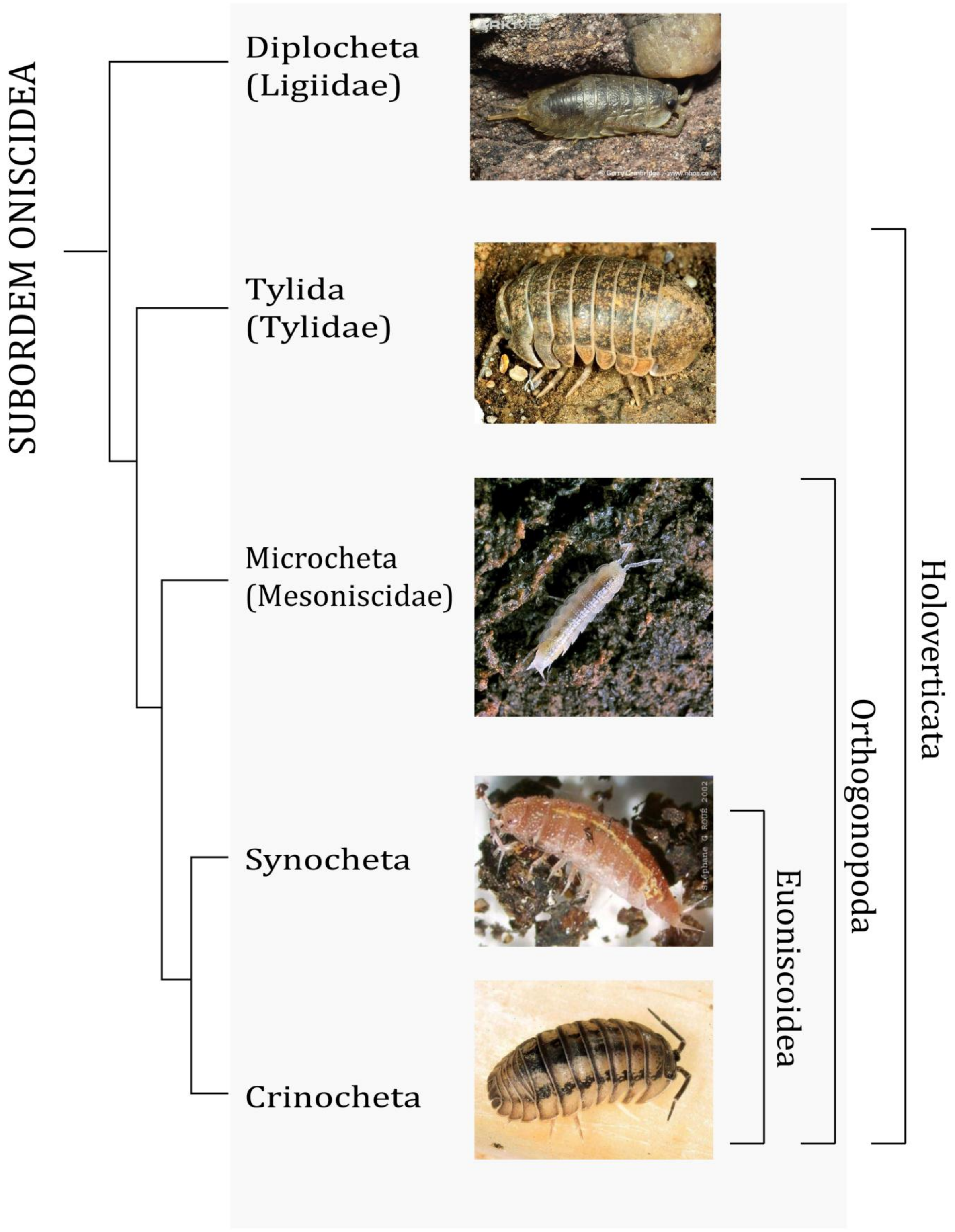

Figura 1. Subordem Oniscidea. Organização da subordem Oniscidea (Crustacea, Isopoda), com suas cinco divisões principais, de acordo com ERHARD (1998).

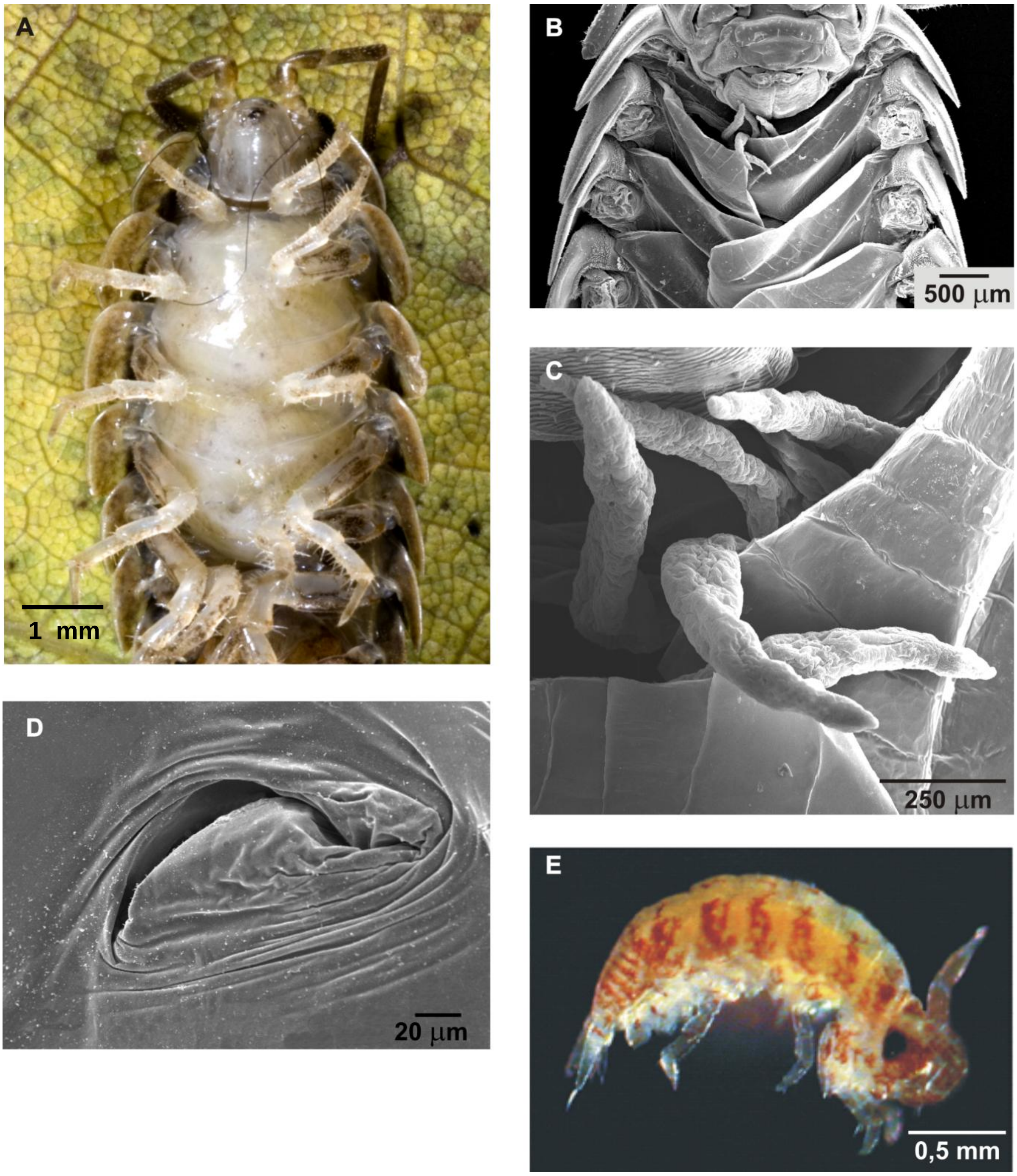

Figura 2. Características da reprodução e desenvolvimento dos Oniscidea. A. Vista ventral geral de uma fêmea com marsúpio (*Balloniscus sellowii*); **B.** Marsúpio de *B. glaber*, mostrando os oostegitos e extremidades de cinco cotilédones; **C.** Detalhe dos cotilédones; **D.** Detalhe (MEV) do poro genital esquerdo de uma fêmea de *B. glaber*; **E.** Manca intramarsupial de *Atlantoscia floridana*.

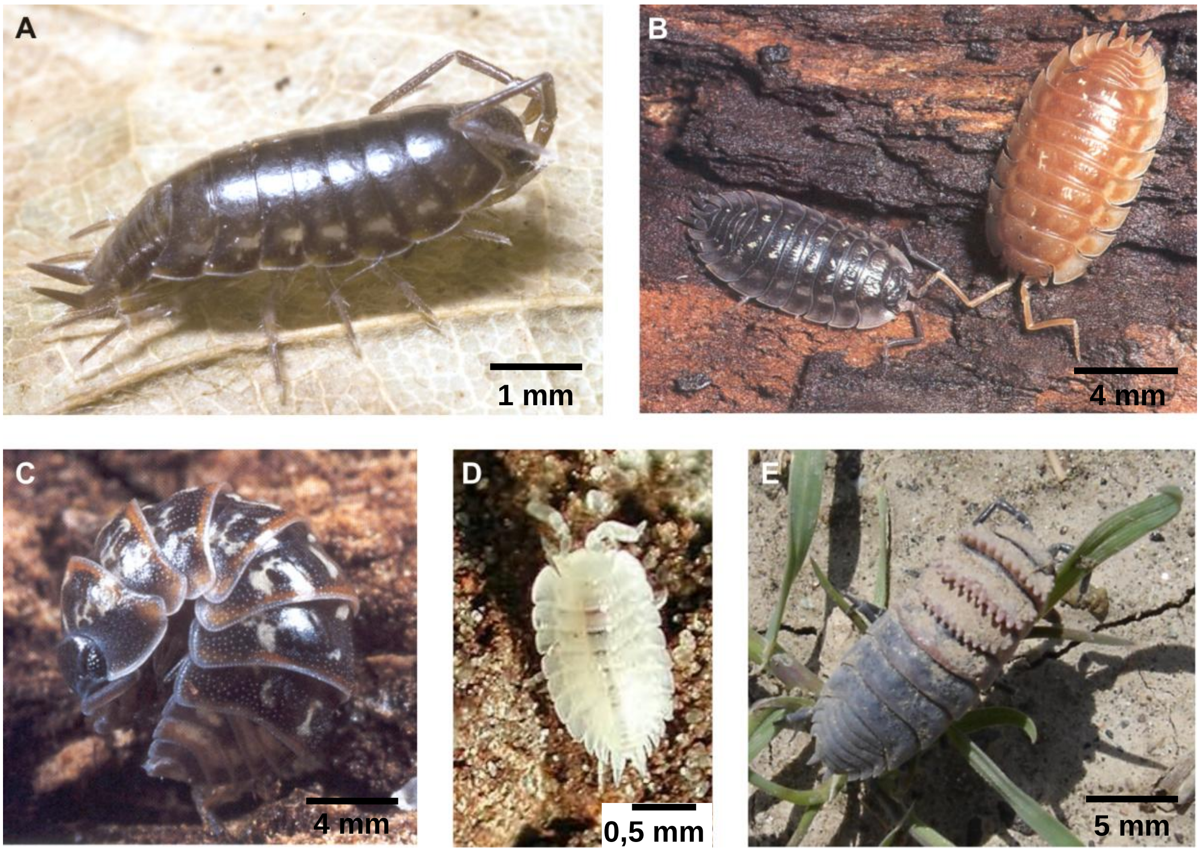

Figura 3. Grupos eco-morfológicos de Schmalfuss (1984). A. "Runners" (*Benthana* sp.); **B.** "Clingers" (*Porcellio scaber*); **C.** "Rollers" (*Armadillidium vulgare*); **D.** "Creepers" (Platyarthridae); **E.** "Non-conformists" (*Hemilepistus* sp.).

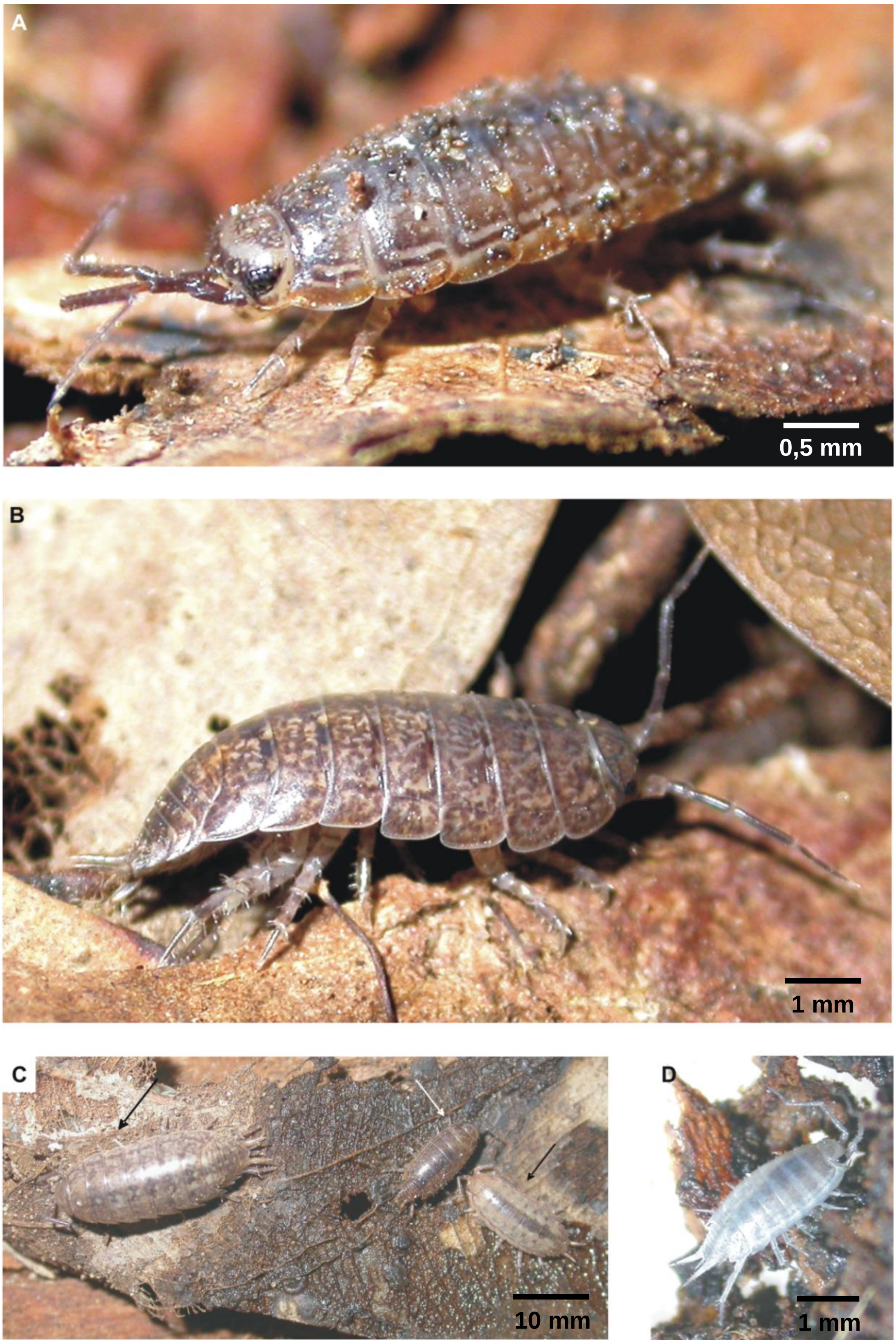

Figura 4. Os modelos de estudo. A. *Atlantoscia floridana*; **B.** *Balloniscus glaber*; **C.** Diferenças de tamanho entre as espécies: adulto de *A. floridana* (seta branca) ao lado de um juvenil de *B. glaber.* Seta preta: indivíduo de *B. glaber* adulto. **D.** *A. floridana* mostrando distrofia pigmentar.

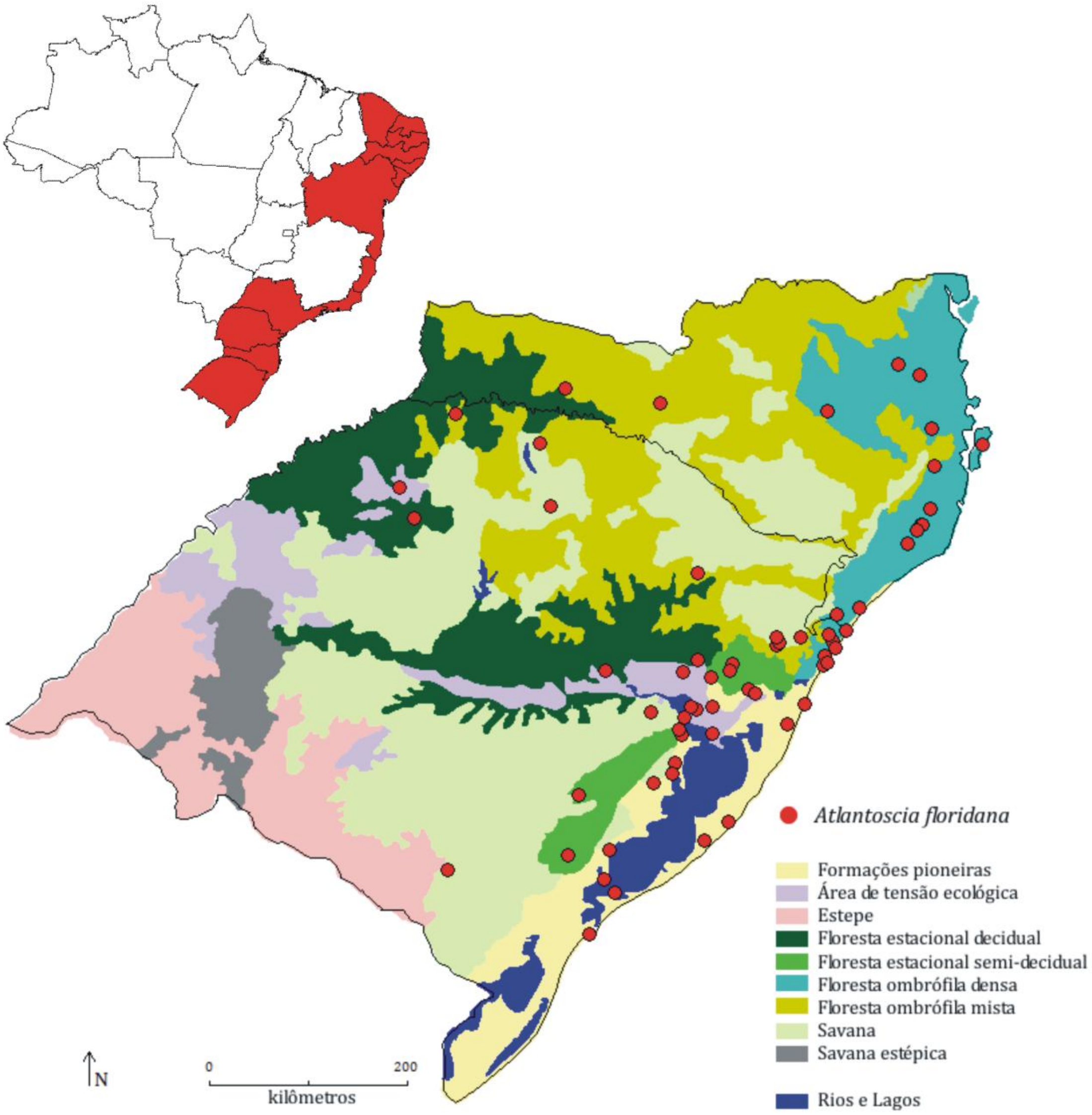

Figura 5. Distribuição geográfica conhecida de *Atlantoscia floridana*. Acima, em vermelho, estão indicados os estados do Brasil com registro de ocorrência da espécie. Abaixo, em detalhe, mapa das formações vegetais dos estados do Rio Grande do Sul e Santa Catarina e as áreas de ocorrência da espécie.

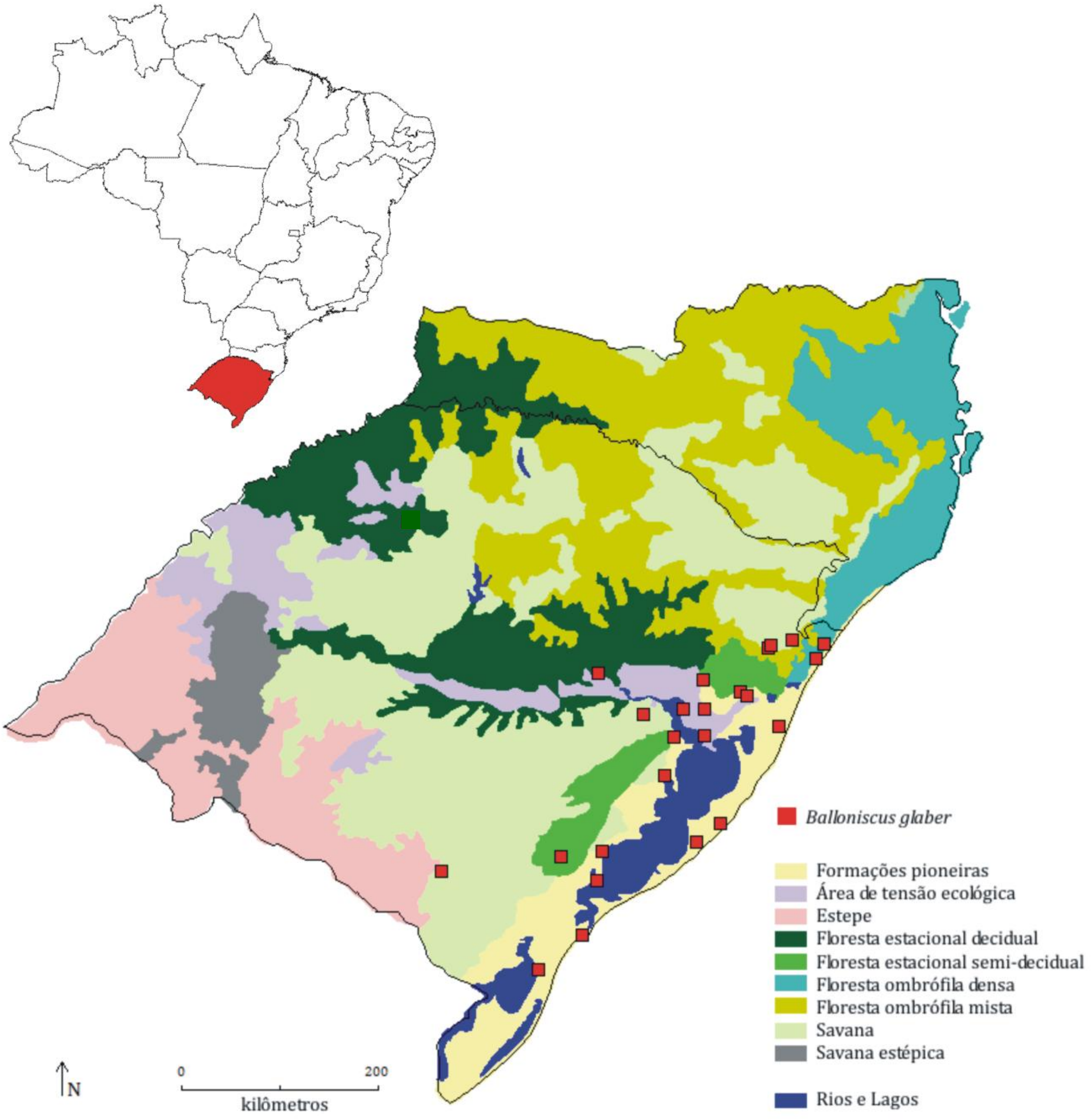

Figura 6. Distribuição geográfica conhecida de *Balloniscus glaber*. Acima, em vermelho, estão indicados os estados do Brasil com registro de ocorrência da espécie. Abaixo, em detalhe, mapa das formações vegetais dos estados do Rio Grande do Sul e Santa Catarina e as áreas de ocorrência da espécie.

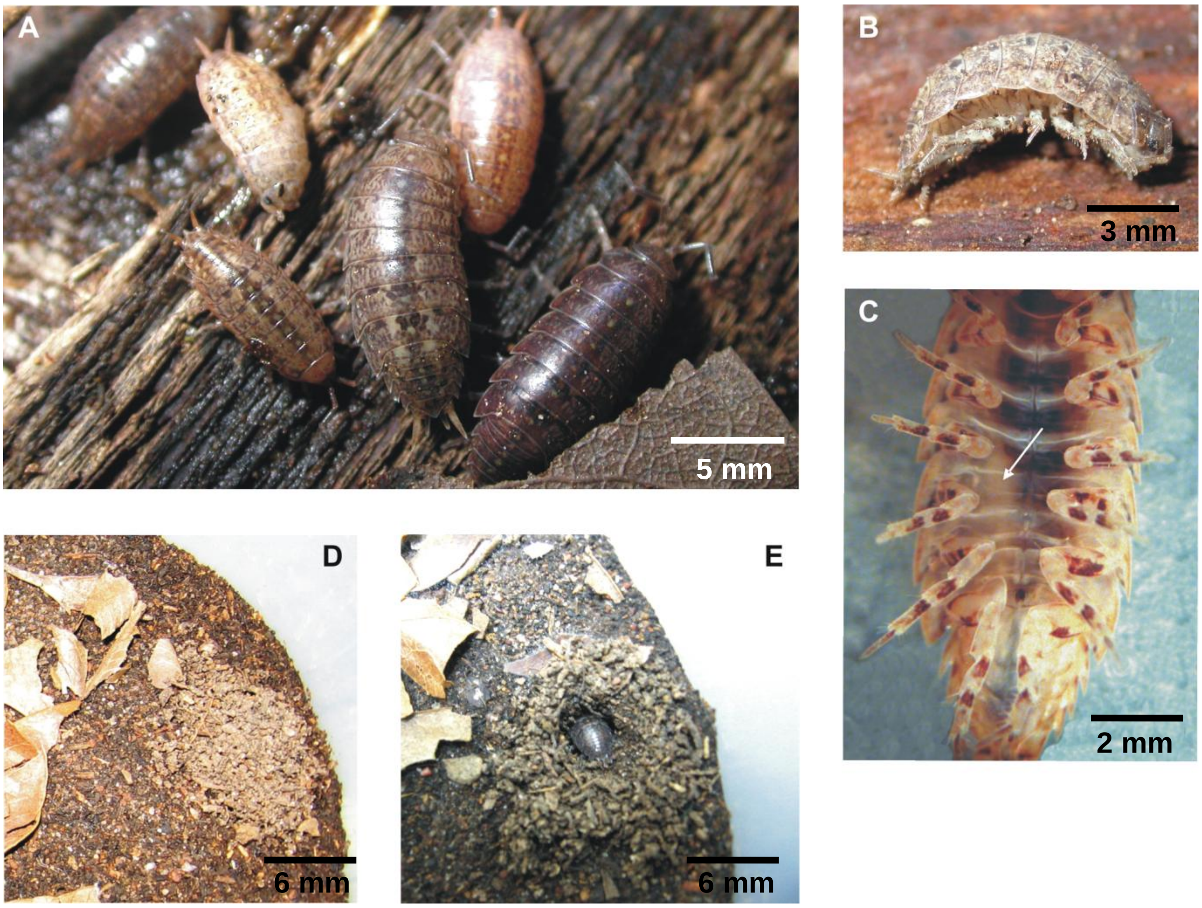

Figura 7. Características ecológicas de *Balloniscus glaber*. A. Polimorfismo de cor; **B.** Tanatose (indivíduo fingindo-se de morto); **C.** Vista ventral de uma fêmea parasitada por um Acanthocephala (seta); **D, E.** Habilidade escavatória. Em D aparece a porção de terra e *pellets* fecais cobrindo o buraco e em E mostra o ocupante do buraco, após a remoção da cobertura.

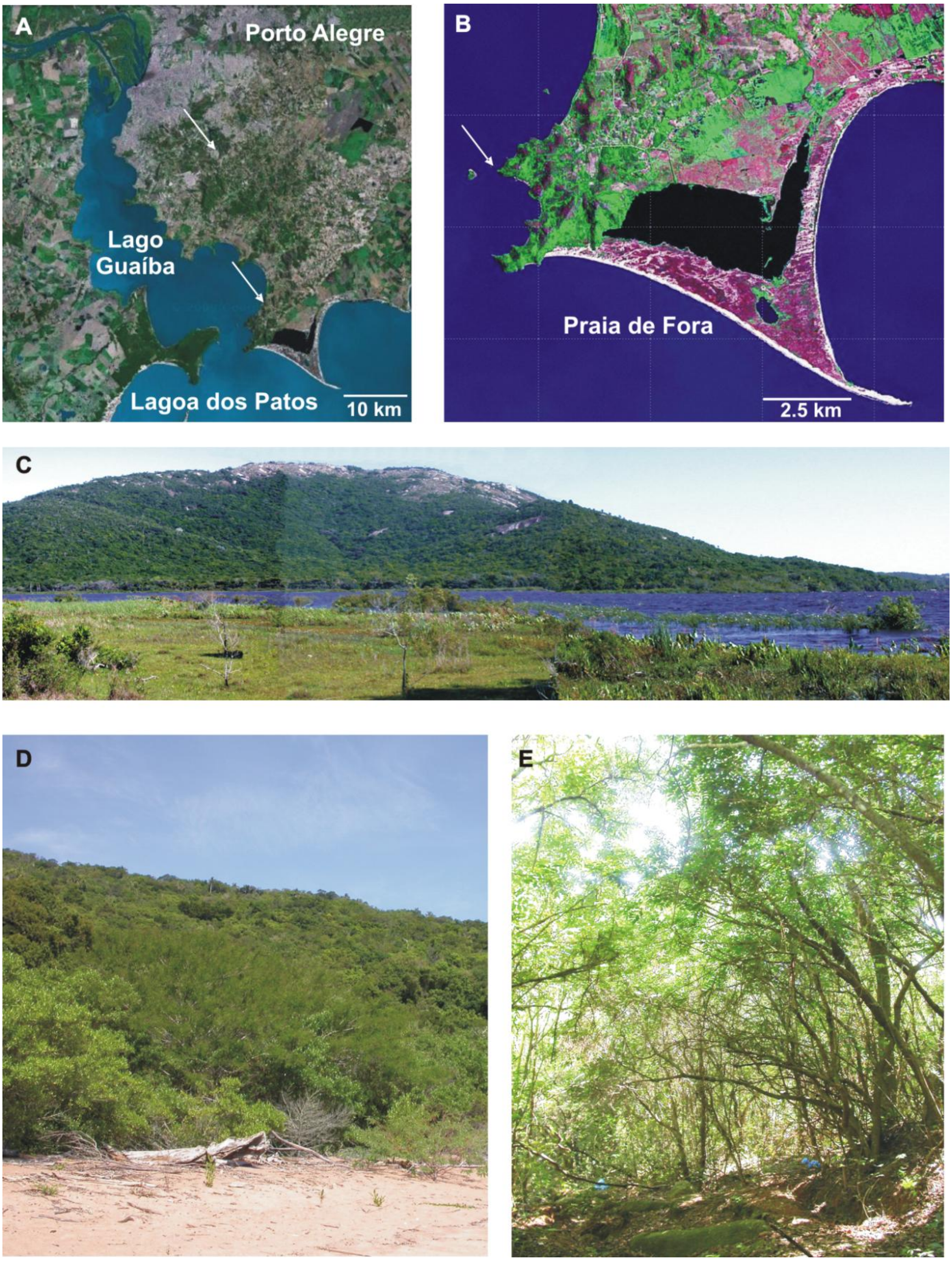

Figura 8. Parque Estadual de Itapuã (PEI). A. Foto de satélite de Porto Alegre, RS, mostrando a localização do Morro Santana (seta de cima) e o PEI (seta de baixo); **B.** Área do Parque, indicando a área de estudo; **C.** Diversidade de paisagens do PEI. Morros graníticos cobertos por floresta, corpos d'água, campos e vegetação de restinga; **D, E.** Detalhes da área de estudo.

Figura 9. Morro Santana. A. Foto de satélite do Campus do Vale da UFRGS, Porto Alegre, RS, indicando o fragmento de floresta utilizado como área de estudo (capítulo 5); **B.** Vista geral do interior da área.

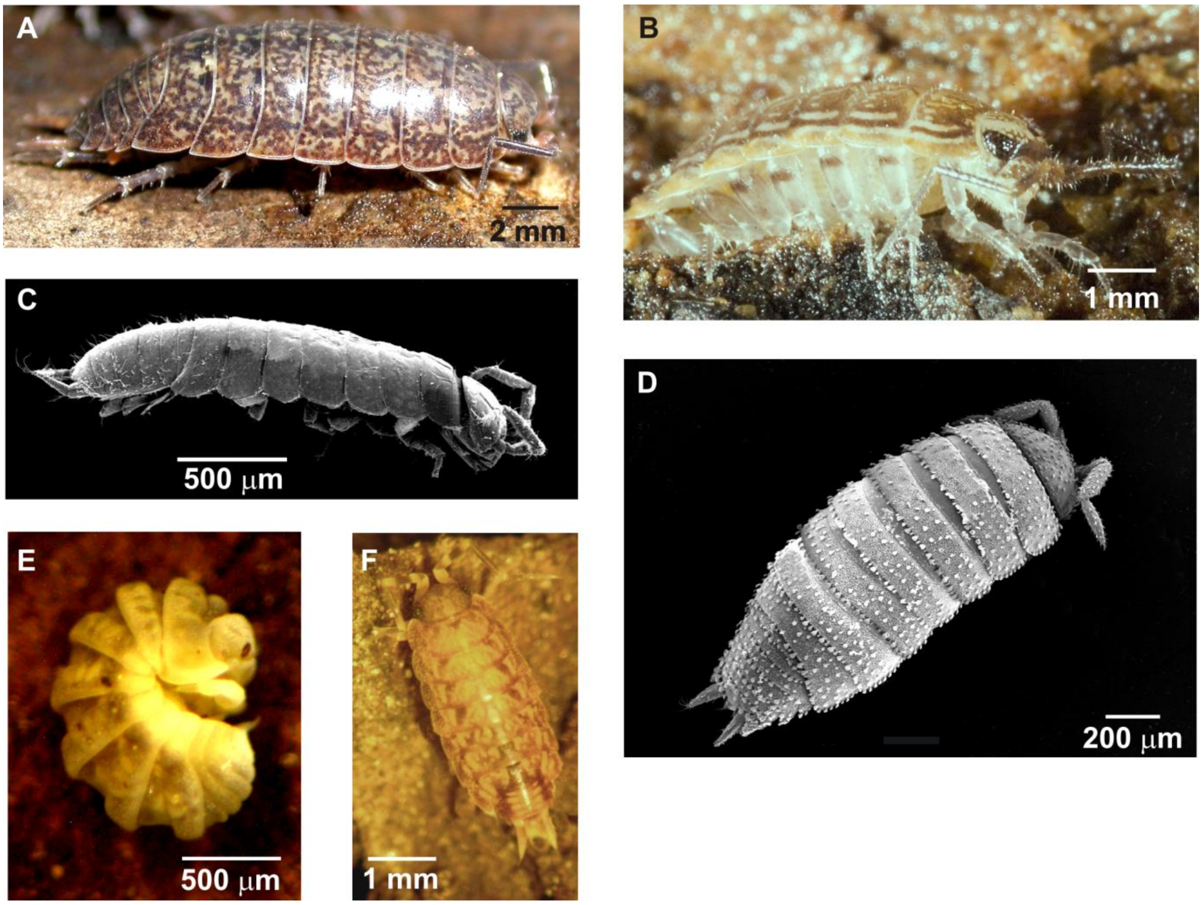

Figura 10. Isópodos terrestres do Parque Estadual de Itapuã (capítulo 1). **A.** *Balloniscus glaber* (Balloniscidae); **B.** *Atlantoscia floridana* (Philosciidae); **C.** *Alboscia itapuensis* (Philosciidae); **D.** *Trichorhina* sp. (Platyarthridae); **E.** *Pseudodiploexochus tabularis* (Armadillidade); **F.** *Novamundoniscus gracilis* (Dubioniscidae).

Créditos das figuras

Figura 1. Ligiidae: Garry Cambridge (www.nhpa.co.uk); Tylidae e Crinocheta: Cezare Brizio (http://tolweb.org/images/Isopoda/6320); Mesoniscidae: (http://www.unesco.eu.sk/dedicstvo/vystava/07panel/panel.html); Synocheta: (http://pagesperso-orange.fr/zenza/cloportes/intro.html);
Figura 2. A: Lucifer©;
Figura 3. A: Lucifer©; B: Stephen Hopkin© 1991; C: Stephen Hopkin© 1991; D: (http://pagesperso-orange.fr/zenza/cloportes/platy.html);E: (http://i1.tinypic.com/8eb2b9e.jpg).
Figura 5. B: Lucifer©; E,F: Adriano Becker.
Figura 8. A: *Google maps*©; B: Foto de satélite LANDSAT. C: Cristiano Iserhard.
Figura 9. A: *Google maps*©

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Capítulo I

“An assemblage of terrestrial isopods (Crustacea) in southern Brazil and their contribution to leaf litter processing”

Conteúdo

QUADROS, AF & PB ARAUJO. 2008. An assemblage of terrestrial isopods (Crustacea) in southern Brazil and their contribution to leaf litter processing. **Revista Brasileira de Zoologia 25**:58-66.

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

ALINE FERREIRA QUADROS[2] & PAULA BEATRIZ ARAUJO[2]

1. Contribution number 503 of Departamento de Zoologia, UFRGS. Project SEMA-RS number 176. 2. Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, IB, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves 9500, Bloco IV prédio 43435, CEP 91501-970, Porto Alegre, RS, Brasil. E-mail: quadros.af@gmail.com; pbaraujo@portoweb.com.br.

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* (Barnard, 1932), *Trichorhina* sp., *Alboscia itapuensis* Araujo & Quadros 2005 and *Novamundoniscus gracilis* Lopes & Araujo, 2003. Total monthly density corresponded to 368 individuals per m^2. 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 laboratory (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} $year^{-1}$.

KEYWORDS. Isopoda; feeding rates; aggregation; species association; eco-morphological groups.

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 6 espécies de quatro grupos eco-morfológicos (em ordem de abundância): *Balloniscus glaber* Araujo & Zardo 1995, *Atlantoscia floridana* (van Name, 1940), *Pseudodiploexochus tabularis* (Barnard, 1932), *Trichorhina* sp., *Alboscia itapuensis* Araujo & Quadros 2005 e *Novamundoniscus gracilis* Lopes & Araujo, 2003. A densidade mensal média correspondeu a 368 indivíduos por m^2. 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. Isopoda; taxas de alimentação; agregação; associação entre espécies; grupos eco-morfológicos.

Introduction

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 m^2 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 m^2 was divided in 12 consecutive sectors (18 m^2). 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 cm^2. From the interior of this recipient, we transferred all vegetal material and the top soil layer ($\approx$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, and 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 ($\mathrm{Log}_{10} + 1$) to minimize the effects of the clumped distribution (ARAUJO & BOND-BUCKUP 2005) and compared with ANOVA. Average density of *A. floridana* and *B. glaber* 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** corresponds 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 5 (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(χ^2/(n + χ^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 aggregation (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 80ºC 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 (≅ 18º 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 2 *B. glaber* individuals and 25 units with 4 *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* Araujo & Zardo 1995, *Atlantoscia floridana* (van Name, 1940) and *Pseudodiploexochus tabularis* (Barnard, 1932) (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 "roller" 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 3 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 Fig 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).

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. 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).

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 Fig 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 Tab. 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 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 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 RS, 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 (pers. obs.).

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 role as detritivores. 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 RS, 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 oniscideans (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 oniscideans 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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Table I. Composition of the studied terrestrial isopod assemblage at Parque Estadual de Itapuã. % TN = % of total number of individuals captured; % TS = occurrence of the species in % 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
BALLONISCIDAE *Balloniscus glaber* Araujo & Zardo 1995	36.1 / 93.7	13.3 mm (male)[1] 13.5 mm (female)[1] Macrofauna	"clinger"	Southern Brazil (RS)[1]
PHILOSCIIDAE *Atlantoscia floridana* (van Name, 1940)	31.2 / 83.3	5.2 mm (male)[2] 7 mm (female)[2] Macrofauna	"runner"	South America[2]
DUBIONISCIDAE *Novamundoniscus gracilis* Lopes & Araujo 2003	0.3 / 4.2	3.6 mm (male)[3] 4.2 mm (female)[3] Mesofauna	undetermined	Southern Brazil (RS)[3]
ARMADILLIDAE *Pseudodiploexochus tabularis* (Barnard, 1932)	26.1 / 71.5	Diameter in volvacion[4] = 2 mm Mesofauna	"roller"	South Africa[4]; Ascension Island[5]; Southern Brazil (RS)[6]
PHILOSCIIDAE *Alboscia itapuensis* Araujo & Quadros (2005)	0.3 / 8.3	2 mm (male)[7] 2.8 mm (female)[7] Mesofauna	"creeper"	Southern Brazil (RS)[7]
PLATYARTHRIDAE *Trichorhina* sp.	6.0 / 39	3 mm Mesofauna	"creeper"	Unknown; probably Southern Brazil (RS)[8]

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
Trichorhina sp.	5.00
P. tabularis	1.75
A .floridana	1.37
B. glaber	0.54

Species		*B. glaber*	*A .floridana*	*Trichorhina* sp.	*P. tabularis*
				L_{AB}	
B. glaber			0.25	0.22	0.28
A .floridana	S_{AB}	2.32		0.001	0.02
Trichorhina sp.		6.19	14.15		0.59
P. tabularis		2.59	6.32	6.55	

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±7.4%	27±3.5%

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, SP)	5900	MEGURO *et al.* (1979)
Semi-deciduous (Jundiaí, SP)	5500	MORELLATO (1992)
Deciduous (Santa Maria, RS)	5100	CUNHA *et al.* (1993)
Semi-deciduous (Campinas, SP)	4500	MARTINS and RODRIGUES (1999)
Semi-deciduous (Ouro Preto, MG)	4000	WERNECK *et al.* (2001)
Semi-deciduous (Ouro Preto, MG)	5300	WERNECK *et al.* (2001)
Deciduous (Santa Maria, RS)	6200	KÖNIG *et al.* (2002)
Average **5275 kg ha^{-1} year^{-1}**		

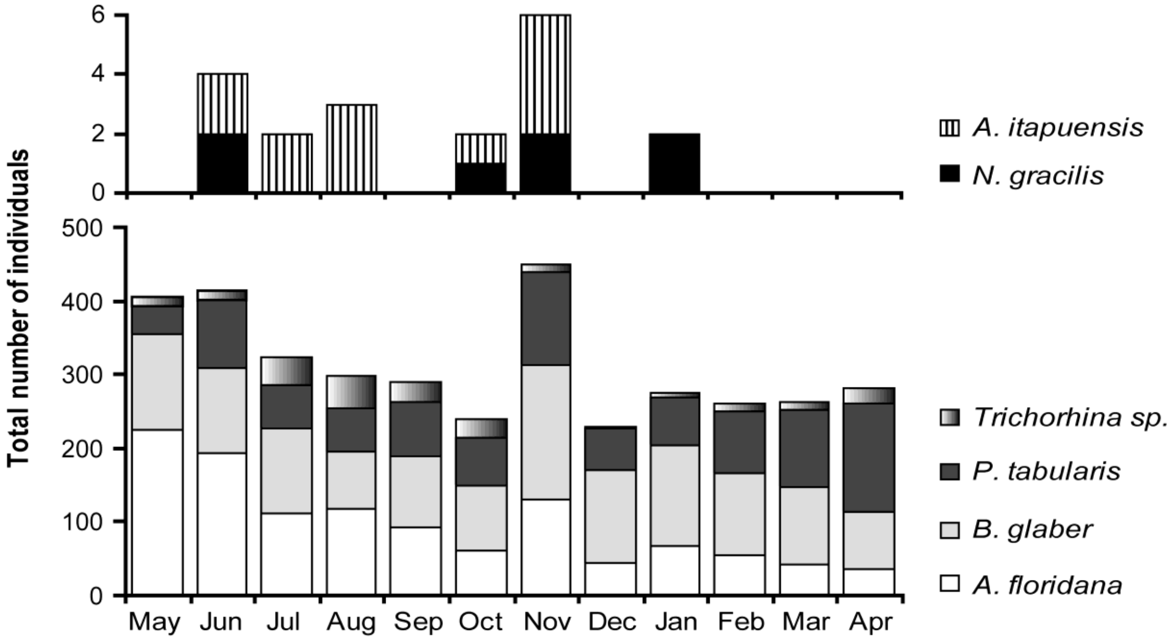

Figure 1. Total number of individuals of terrestrial isopods captured monthly at Parque Estadual de Itapuã, from May 2004 to April 2005.

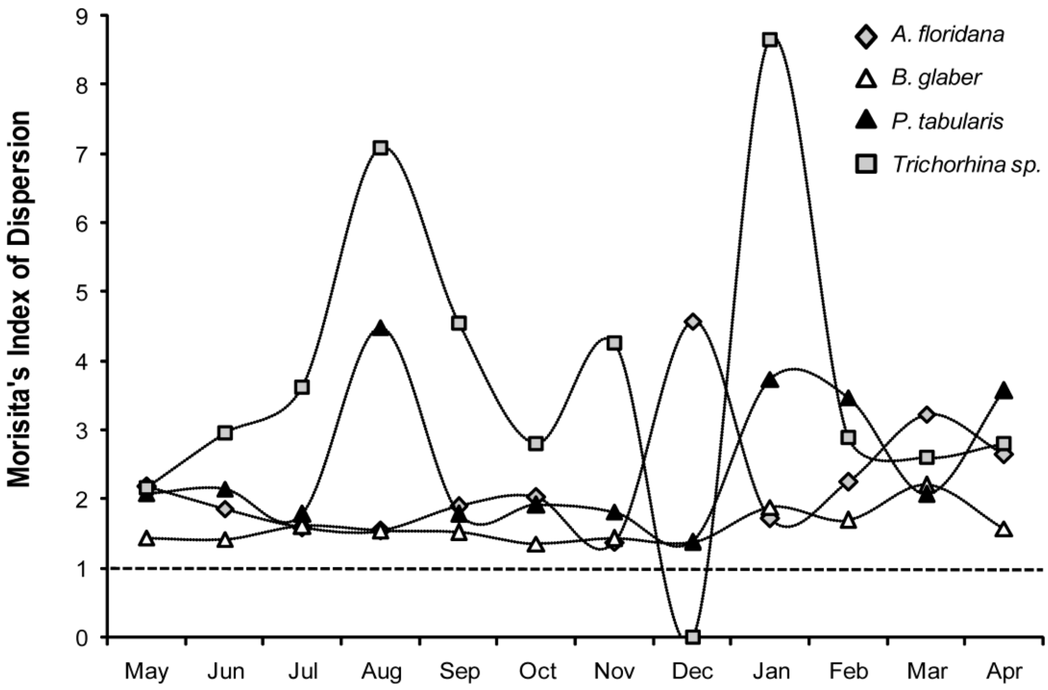

Figure 2. Isopod spatial distribution (Morisita's index of dispersion) in Parque Estadual de Itapuã, from May 2004 to April 2005. Values higher than 1 indicate an aggregate (contagious) distribution.

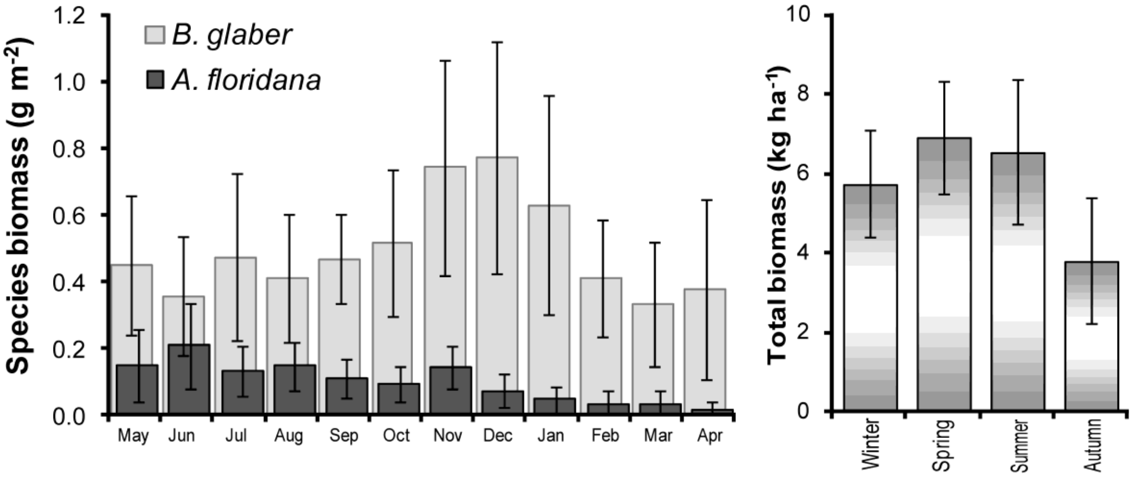

Figure 3. Biomass of *Atlantoscia floridana* and *Balloniscus glaber* at Parque Estadual de Itapuã, between May 2004 and April 2005 (on the left) and the summed biomass of the two species per season (on the right). Values are mean±95% confidence intervals.

Capítulo II

"Ecological traits of two neotropical oniscideans (Crustacea, Isopoda)"

Conteúdo

Quadros, AF & PB Araujo. 2007. Ecological traits of two neotropical oniscideans (Crustacea: Isopoda).
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Ecological traits of two neotropical oniscideans (Crustacea, Isopoda)

ALINE FERREIRA QUADROS[1] & PAULA BEATRIZ ARAUJO[2]

Affiliation:

Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, IB, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, pr. 43435, 91501-970, Porto Alegre, RS, Brasil, 1. quadros.af@gmail.com, 2. pbaraujo@portoweb.com.br.

Abstract

Two terrestrial isopods, *Atlantoscia floridana* (Philosciidae) and *Balloniscus glaber* (Balloniscidae) that differ in size, morphology and behaviour were studied with respect to the influence of the environmental variation on their reproduction and population structure. Samples were taken at Parque Estadual de Itapuã, Brazil from May 2004 to April 2005. Twelve cores of litter and soil were extracted each month, and hand-searched in the lab. All specimens were sexed and measured. Overall, 2540 individuals were captured. *Atlantoscia floridana* reproductive females were present throughout the year, while *B. glaber* showed a shorter reproduction period, from early spring to early autumn, and both species showed high numbers of reproductive females and mancas during spring. Mean density of *A. floridana* was 114 ind. m^{-2} and 133 ind. m^{-2} for *B. glaber.* The increased dryness observed in the summer of 2005 affected the populations differently, as it reduced population size of *A. floridana* while *B. glaber* population remained stable. It seems that the differences in morphology, more specifically body size and presence of pleopodal lungs, confer to *B. glaber* a higher tolerance to desiccation. Moreover, *B. glaber* may rely on behavioral strategies, as burrowing, to increase the survival of the young, and even the survival of the adults under stressful climatic conditions. It is postulated that the continuous reproduction, lower time to maturity and higher proportion of reproductive females of *A. floridana* are responses to its high juvenile mortality.

KEYWORDS neotropical oniscideans, eco-morphological groups, juvenile mortality, tolerance, dessication

Introduction

Some assemblages of terrestrial isopods are composed by several species that aggregate in soil patches in high densities. These species often differ markedly in morphology and life habits (Hornung, 1990; Ma et al., 1991; Zimmer, 2003) and possess different levels of adaptations to the terrestrial life due to morphological specializations of the marsupium (Lewis, 1990), cuticule and respiratory apparatus (Warburg, 1987; Wright and Machin, 1993). These adaptations are likely to affect their population stability (Sutton, 1968), which in turn has an important influence on reproductive strategies (Stearns, 1976). Therefore, populations of coexisting species that differ in morphology often show a variety of life strategies to face the same environmental situations, and differ in traits such as abundance, length of breeding season, number of breeding episodes, age at maturity and life span (Sutton, 1968; Sutton et al. 1984; Ma et al., 1991; Warburg, 1994).

In southern Brazil, two Neotropical isopod species that differ in morphology, body size and behaviour are frequently found in syntopy. The philosciid *Atlantoscia floridana* (van Name, 1940) has a small body size (7 mm long) and a thin and soft cuticle, as compared to the other species, *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae). It has no pleopodal lungs, only respiratory area in exopod of pleopod 1 (Leistikow and Araujo, 2001) and runs if disturbed – a behaviour allowed by the combination of long pereopods and a narrow body shape – a “runner” type (sensu Schmalfuss, 1984). The isopod *B. glaber* is 14 mm long, has 5 pairs of pleopodal lungs, and remains motionless if disturbed, “pretending to be dead” – a “clinger” type (sensu Schmalfuss, 1984). Furthermore, *A. floridana* is abundant and widespread along the coast of Brazil (Araujo and Bond-Buckup, 2005), where it is found in natural and anthropic habitats, often in high densities (≈ 450 ind. m^{-2}) while *B. glaber* has a restricted distribution, occurring only in the southernmost Brazilian state (Araujo and Zardo, 1995).

Based on the above characteristics, we believe these species to have developed different strategies to face common environmental conditions. We expect *A. floridana* to be found in higher densities than *B. glaber*, although its population should be more unstable along the year, as *A. floridana* may have less environmental tolerance, judging from its smaller size, thin exoesqueleton and the possession of less specialized respiratory structures. In order to verify this, we compared the changes in abundance, reproduction and population structure in these two species, along one year.

Material and Methods

Study area

The Parque Estadual de Itapuã (PEI) is a protected area of 5,566 ha located in the metropolitan area of Porto Alegre, Rio Grande do Sul, Brazil, destined to the preservation. The landscape of the PEI comprises dunes, lagoons, granite hills, grasslands, and forests (Rio Grande do Sul, 1997). The climate is humid subtropical, Köppen’s Cfa type (Strahler, 1974), with significant precipitation during all seasons (annual rainfall of 1300 mm), annual mean air temperature of 17.5°C (Rio Grande do Sul, 1997), and mean maximum and minimum are 30.6oC and 11.3oC, respectively (Embrapa, 2006).

This study was carried on a hill slope near the coastal lagoon beach “Praia da Onça” (30º34’S 51º05’W). This portion of the hill is composed of a semi-deciduous forest with 2 to

3 arboreal strata 10 to 15 m high and the diameter at breast height >5 cm (Brack et al., 1998). The leaf litter was derived mainly of dicotyledonous plants.

Sampling

Samples were collected monthly from May 2004 (late autumn) to April 2005 (mid autumn), always between 0900 and 1100 a.m. Sampling design followed Araujo and Bond-Buckup (2005). The study site consisted of a 36-m long and 6-m wide area, divided into 12 consecutive 3-m long and 6-m wide quadrants. Twelve cores (one per quadrant) were sorted each month (totaling 144 cores), and a circular bottomless recipient of 30 cm diameter was used to extract the litter and soil to plastic bags. In the laboratory, the content of those bags was hand-searched to separate the isopods. After this first examination, the content was left in a Berleze Funnel for 72 h, to ensure that all the mancas and smaller individuals were caught. For the analysis of microclimatic variables, we took three measures of litter and soil (3 cm deep) temperature and three samples of litter and soil for water content determination by the gravimetric method (Allen, 1984). These procedures were performed at 1100 a.m.

Laboratory procedures

We recorded the counts of mancas (MC), males (MA) and females (FE) in each core. Females were considered as non-reproductive (NR; without marsupium) or reproductive (RF), the latter including both ovigerous (OV; marsupium with content) and post-ovigerous females (PO; empty marsupium). We recorded the fecundity (number of eggs inside the marsupium) for all OV. We measured the cephalothorax width (CW) of all individuals with a stereomicroscope (0.01 mm accuracy) (Sunderland et al., 1976; Araujo and Bond-Buckup, 2004).

Analyses

Long-term (1961-2005) mean values of precipitation and air temperature were obtained from INMET (2006) and those for the study period (2004-2005) were obtained from Embrapa (2006).

We used the coefficient of variation (CV) to express the variation of litter/soil temperature (°C) and water content (%) during the experimental period. We applied a multiple regression to assess the relationship between these parameters and density: soil/litter temperature and water content were treated as the independent variables and density as the dependent variable. We compared the densities (Log_{10}) between seasons, within and between species, using the Kruskal-Wallis test after checking the homoscedasticity of variances.

We defined the range of the size classes based on one-fourth of the standard deviation of the mean size of males and females pooled (Markus, 1971). We estimated the corresponding mean age for each size class using the von Bertalanffy's growth curves provided by Araujo and Bond-Buckup (2004) for *A. floridana* (CW_t females$=1.682(1-e^{-0.00575(t+59.13)})$) and ($CW_t$ males$=1.303(1-e^{-0.00941\ (t+50.37)})$) and P.B. Araujo (pers. com.) for *B. glaber* (CW_t females$=2.588(1-e^{-0.00301(t+101.0)})$) and ($CWt$ males$=2.256(1-e^{-0.00394(t+91.128)})$). In these equations, CW_t stands for the cephalothorax width (mm) of the individual and t is the correspondent age in days. The length of the size classes and the respective estimated mean age of males and females of both species are listed in Table 1.

We considered females of both species as adults based on the size of the smallest ovigerous female found during the entire sampling period. Moreover, we differentiated Potential Reproductive Females (PRF; the number of adult females out of total females found per month) from Actual Reproductive Females (ARF; representing the number of reproductive females out of the number of PRF). According to Araujo et al. (2004), *A. floridana* male size at the onset of sexual maturity is 0.79 mm (CW) and this information was used to discriminate between male juveniles and adults. As such information was not available for *B. glaber*, its males were not treated separately.

In order to quantify the commitment of each population to reproduction during a year, we calculated an Index of Reproductive Mobilization (IRM) of each population. We considered that the maximum mobilization would be achieved if 100% of the females of a month where adults, therefore PRF=1, and from these, 100% were reproductive, i.e. ARF=1, and they were bearing the maximum mean fecundity recorded through the year. Multiplied, these three parameters give the IRM_{max} of each species. The observed IRM for each month was calculated as [(PRF x ARF x mean fecundity) x 100/IRM_{max}].

Results

Microclimatic variables

During the study period, most months had less rainfall than expected, with increased dryness between Nov-Feb. In December rainfall was 18 mm, much lower than the long-term mean precipitation for this month (96 mm), and, during Jan-Feb, it was about 29% of the expected for the period (Fig. 1). Air temperature, however, matched the long-term predictions (Fig. 1).

Regarding water content, soil was more variable than litter along the year, as indicated by the coefficient of variation. Soil water content ranged from 8 to 60% (CV=71%) and litter water content ranged between 20-73% (CV=52%). Soil temperature ranged from 12.6°C to 23.2°C (CV=17%) and litter temperature ranged from 14.2°C to 24.7°C (CV=15%).

During the coldest and the most humid period (winter) litter water content was 40% and litter temperature was 16.5°C. During the driest period (summer), litter and soil water content averaged 21% and 10%, respectively, and litter temperature reached 23.2°C (Fig. 1).

Abundance

Overall, 2540 individuals were captured, out of which 46% were *A. floridana* and 54% were *B. glaber*.

During the study year, the abundance of *A. floridana* was more variable (CV=61%) than that of *B. glaber* (CV=26%). However, contrary to our expectations, mean densities of the species were similar: 133 (±107 s.d.) ind. m^{-2} for *B. glaber* (range: 14 to 500 ind. m^{-2}) and

114 (±140) ind. m^{-2} for *A. floridana* (range: 14 to 800 ind. m^{-2}). Through the year, densities did not differed during winter (Kruskal-Wallis H=0.9087, P>0.3) and spring (Kruskal-Wallis H=2.4932, P>0.1), and *B. glaber* outnumbered *A. floridana* during summer and autumn (Kruskal-Wallis H=12.9208, P<0.01 and H=6.2347, P=0.01, respectively)(Fig. 1). The highest monthly density of *A. floridana* was observed in May (252 ind. m^{-2}), and Nov in the case of *B. glaber* (221 ind. m^{-2}) (Fig. 1).

The significant decrease observed in the density of *A. floridana* between the winter of 2004 and the summer of 2005 (Kruskal-Wallis H=25.8082, P<0.0001) (Fig. 1) was correlated with a decrease in soil water content (Multiple R^2=0.89, F=6.9217, P=0.01). The density of *B. glaber* did not differed among seasons (Kruskal-Wallis H=3.2302, P>0.3), and there was no correlation with the considered abiotic parameters (Multiple R^2=0.39, F=0.3153, P>0.3).

Reproduction

The smallest ovigerous female found during the entire sampling period was 1.12 mm (CW) for *A. floridana* (≈ 4 months old; Table 1) and 1.62 mm for *B. glaber* (≈ 7 months old; Table 1). The highest mean fecundity was 14 for *A. floridana* and 16 in the case of *B. glaber* and these values were used to compose the IRMmax of the species.

Atlantoscia floridana RFs were present throughout the year, and their density varied from 1 to 33 ind. m^{-2}. *Balloniscus glaber* showed a shorter reproduction period – from early spring to early autumn and the density of their RF varied from 1 to 26 ind. m^{-2} (Fig. 2). The density of RF of both species was maximal in Nov (Fig. 2).

Atlantoscia floridana usually presented higher PRF, ARF and IRM proportions as compared to *B. glaber* (Table 2). In December 96% of *A. floridana* were PRF and a high percentage (83%) was in reproduction, and 50% of its maximum IRM was achieved during this period (Table 2). November was also important, as it had a high percentage of ARF (85%), and also the second highest IRM, 27% (Table 2).

The absence of *B. glaber* ovigerous females between May-Aug was not due to the absence of PRF, which, in fact, accounted for 20% of total females of this period. When reproduction started in Sep, only 23% of the females were PRF, and in Nov, they represented 68% of the females. However, the highest ARF, 63%, was observed in Oct (Table 2).

Mean density of mancas ranged from 2 to 58 ind. m-2 for *A. floridana*, and from 1 to 104 ind. m-2 for *B. glaber*, the highest density being observed in Nov (Fig. 2). About 50% of RF and 46% of mancas of both species were found in spring. Interestingly, there was an outbreak of *B. glaber* mancas in Nov, with 45% of its total being captured at this time. *Atlantoscia floridana* mancas were found almost every month and also peaked in Nov (34%). The mancas:RF ratio was 1.2 for *A. floridana*, and 2.6 for *B. glaber*.

Differently from *A. floridana*, whose mancas already presents the adult pattern of pigmentation, it was noticed that *B. glaber* young are pigment-less and remain as this through the first juvenile stages. The *B. glaber* adults have a very dark-brown pigmentation.

Population structure

When this study started in May, the *A. floridana* population (Fig. 3, left) was composed by almost all classes of individuals, being 13% mancas, 40% juveniles, and 47% adults. The RF were present in classes XIII to XIX, i.e., from 5 to 12 months of age. In Jul, there was intense mortality of juvenile females and reproduction ceased, since there were no mancas in Aug. In Sep, most RF were 6 months old, and towards Dec there was an intense mortality of both male and female juveniles and male adults. This picture was later reversed, as in Feb-Apr almost all adult females died. Most RF in Nov were 7 months old, thus were most were probably hatch in May of the same year.

Balloniscus glaber population (Fig. 3, right) at the end of the autumn consisted mainly of juvenile females, and male distribution was bimodal: one peak around class VIII (3.6 months), and one around class XV (14.8 months). Mancas were practically absent from Jun to Oct. In Nov, the highest RF frequency was observed. As these RF were between 8 and 12 months of age (classes XII to XV), they were probably hatch during the previous summer. Individuals of the first juvenile stages (classes 2 to 4) were seen from Dec on, and between Jan and Apr the size distribution became clearly bimodal. Reproductive females older than 13 months (classes XVI-XVIII) were seen mostly during the summer, and there was no RF present in the classes XIX and XX, i.e., 2 years-old or more.

Discussion

Contrary to our expectations, the density of *A. floridana* was lower than expected based on our previous observations and on the literature (Araujo and Bond-Buckup, 2005). However, as we predicted, its population was more unstable, in terms of abundance and population structure, as compared to *B. glaber*. Regarding reproductive traits, the species differed in the length of their reproductive season, age at maturity and frequency of breeding females, while in spite of the large difference in the size of the reproductive females, their fecundity was similar. The observed combination of reproductive traits of each species seems to be correlated with the influence that climate exerts in each population.

By reproducing only in spring and summer, *B. glaber* resembles the majority of terrestrial isopods species, which usually reproduce only during the warmer months (Sutton, 1968; Hornung, 1990; Warburg, 1994; Zimmer, 2004). Temperature is an important factor influencing the timing of the reproduction of terrestrial isopods, as it stimulates breeding (Madhavan and Shribbs, 1981), accelerates juvenile growth (Helden and Hassall, 1998) and shortens brooding period (Snidder and Shaddy, 1980). This response to temperature is independent of morphology or life style of the species, given that a highly overlapped reproductive timing has been reported between sympatric species of different eco-morphological groups (Sutton et al., 1984; Zimmer, 2004). However, *A. floridana* differs from that pattern as its population maintains a continuous reproduction along the year, as already observed by Araujo and Bond-Buckup (2005) for a population of a different site.

The causes of this continuous reproduction may be related to the mortality of the young. Dangerfield and Telford (1995) observed repeated reproduction amongst tropical isopods and suggested that it would be favored in an environment with a high juvenile mortality. Accordingly, life history theory predicts that iteroparity would be directly selected for whether the risk of total reproductive failure is significant, and the degree of iteroparity (number of breeding seasons) is positively correlated with the ratio of juvenile mortality to adult mortality (Stearns, 1976).

Although we have no direct information on mortality rates, the mortality of *A. floridana* mancas and juveniles can be depicted from its population structure. During the study year, the summer dryness visibly affected the smallest classes of individuals, as well as the adult/reproductive females. Moreover, the number of mancas was low as compared to the proportion of reproductive females in the population, and the number of individuals entering the first juvenile classes was even lower, as compared to the number of mancas (and as compared to *B. glaber* population). Thus, we infer that, as compared to *B. glaber*, *A. floridana* presents a higher degree of iteroparity and higher reproductive mobilization as a response for the high mortality of its young as a consequence of its lower resistance to desiccation.

The higher tolerance exhibited by *B. glaber* may be attributed, at least to some extent, to the presence of pleopodal lungs, allowing for a more efficient respiration (Schmidt and Wägele, 2001) and to its larger size, accounting for a lower surface to volume ratio. Regarding differences in size, Sutton (1968) described a similar trend between two sympatric oniscidean species. *Philoscia muscorum* (Scopoli, 1763), the larger species, was indifferent to drought by means of a higher physiological tolerance and *Trichoniscus pusillus* (Brandt, 1833), the smaller species, was able to survive the extremes of climate through vertical migration and an extending breeding (Sutton, 1968).

In addition to morphological features, behavioral strategies may also enhance the survivorship of *B. glaber*. Edaphic arthropods that are sensitive to desiccation may escape adverse conditions by moving into more favorable microhabitats, such as the soil (Villani et al., 1999). Vertical migration under moisture gradients was shown for northern hemisphere isopods (Warburg, 1987), as well as for other arthropods (Villani et al., 1999). Both field and laboratory observations showed that *B. glaber* is an endogean species (Araujo and Zardo, 1995), which is reinforced by the fact that their young lack pigmentation. The absence of pigmentation is common in small endogean isopod species, such as *Haphlothalmus danicus* Budde-Lund, 1880 and *Trichorhina* spp.

Sutton et al. (1984) provided a series of life history predictions for terrestrial isopods, grouping them into two broad categories, the 'soil-active' and 'surface-active' species. *Balloniscus glaber* seems to match the predictions made for the former group, which include small proportion of breeding females, slow rate of growth and long time to maturity, small number of young (Sutton et al., 1984) and these traits also supports for lower juvenile mortality (Stearns, 1976). In this study we illustrate the proportion breeding as the ARF, which for *B. glaber* was much lower than *A. floridana*. The slower growth rate and thus long time to maturity can be seen in the von Bertalanffy's growth equations given in the literature (0.00301 for *B. glaber* females and 0.00575 for *A. floridana* females; Araujo and Bond-Buckup, 2004). With respect to fecundity, the low number of *B. glaber* females achieving two years of age indicates that they experience only one reproductive year and their mean fecundity is much lower as compared to species of similar size such as *Armadillidium nasatum* Budde-Lund, 1885, and as compared to other "clinger" species as *Porcellio scaber* Latreille, 1804 and *Trachelipus rathkii* (Brandt, 1833) (Glazier et al., 2003).

The reproductive patterns of both species reflect their differential survivorship, as *A. floridana* starts to reproduce earlier and presents a high proportion of reproductive females along the entire year while *B. glaber* shows a delayed maturity, low fecundity and smaller proportion of reproductive females, and notwithstanding, a higher density of young individuals. It seems that the differences in morphology, more specifically larger body size and presence of pleopodal lungs, confers to *B. glaber* increased levels of tolerance to desiccation, as compared to *A. floridana*, and additionally, this species may rely on behavioral strategies to increase the survival of the young, and even the survival of the adults under stressful climatic conditions.

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Table 1. Size (cephalothorax width) and age classes for *Atlantoscia floridana* and *Balloniscus glaber*. Age estimates are based on the von Bertalanffy growth curves provided in the literature. Class I represents the mancas, m=males, f=females.

	Atlantoscia floridana			*Balloniscus glaber*		
		Mean age (days)			Mean age (days)	
Class	**Size (mm)**	M	F	**Size (mm)**	M	F
I	—| 0.53	undifferentiated		—| 0.77	undifferentiated	
II	—| 0.63	13	16	—| 0.82	20	22
III	—| 0.68	24	27	—| 0.91	32	34
IV	—| 0.73	32	35	—| 1.01	50	53
V	—| 0.79	43	45	—| 1.10	69	73
VI	—| 0.84	54	56	—| 1.19	89	93
VII	—| 0.89	66	66	—| 1.28	110	115
VIII	—| 0.94	79	77	—| 1.38	135	139
IX	—| 0.99	93	89	—| 1.47	163	165
X	—| 1.05	112	103	—| 1.56	192	192
XI	—| 1.10	135	118	—| 1.66	227	223
XII	—| 1.15	162	133	—| 1.75	267	256
XIII	—| 1.20	198	150	—| 1.84	313	292
XIV	—| 1.25	254	168	—| 1.93	369	333
XV	—| 1.30	436	188	—| 2.03	446	381
XVI	—| 1.36	—	213	—| 2.12	557	438
XVII	—| 1.41	—	243	—| 2.21	758	502
XVIII	—| 1.46	—	275	—| 2.30	1138	583
XIX	—| 1.51	—	315	—| 2.40	—	699
XX	—| 1.56	—	367	—| 2.49	—	877
XXI	—| 1.62	—	455	—	—	—

Table 2. Potentially reproductive females (PRF; number of adult females/total females), Actual reproductive females (ARF; number of reproductive/total adult females) and the Index of Reproductive Mobilization (IRM; % of IRMmax) of *Atlantoscia floridana* and *Balloniscus glaber*.

	Atlantoscia floridana			*Balloniscus glaber*		
	PRF	ARF	IRM	PRF	ARF	IRM
May	0.46	0.27	9%	0.17	0.00	0%
Jun	0.31	0.18	4%	0.13	0.00	0%
Jul	0.41	0.04	1%	0.24	0.00	0%
Aug	0.43	0.31	9%	0.24	0.00	0%
Sep	0.69	0.47	19%	0.23	0.20	3%
Oct	0.66	0.44	20%	0.40	0.63	25%
Nov	0.55	0.85	28%	0.68	0.48	22%
Dec	0.96	0.83	50%	0.61	0.23	11%
Jan	0.42	0.67	15%	0.40	0.50	16%
Feb	0.15	0.75	11%	0.44	0.25	9%
Mar	0.11	0.00	0%	0.16	0.57	6%
Apr	0.14	1.00	4%	0.23	0.08	0%

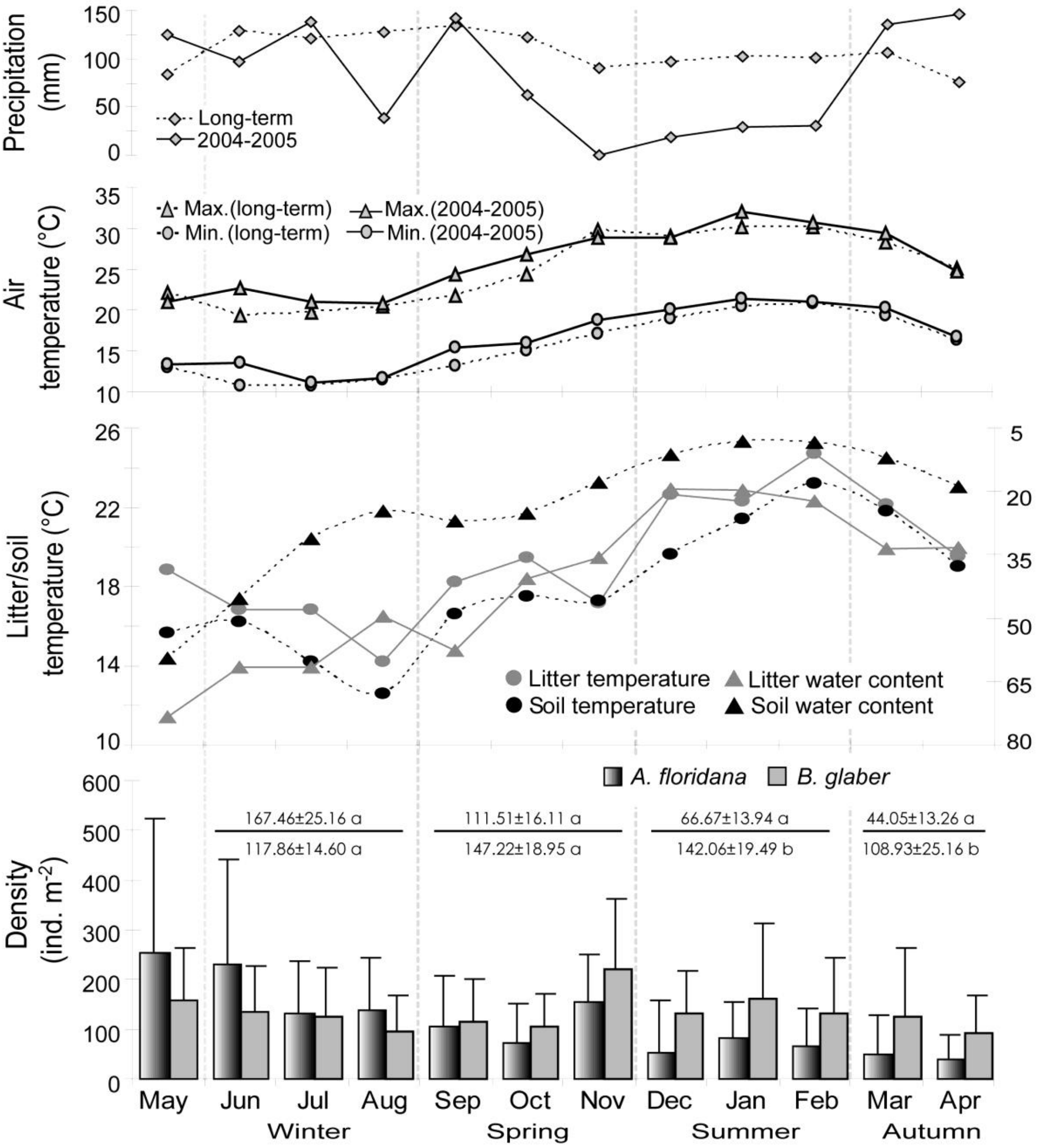


Figure 1. Microclimate and density of *Atlantoscia floridana* and *Balloniscus glaber* at Parque Estadual de Itapuã, Brazil, surveyed from May 2004 to April 2005. Except for precipitation, all values are averages. Long-term means refer to the period 1961-2005. Vertical lines refer to seasons. Values above and bellow the horizontal lines refer to the mean density ± S.E. of *A. floridana* and *B. glaber*, respectively, and different letters indicates differences between the two species (Kruskal-Wallis, $p<0.05$).

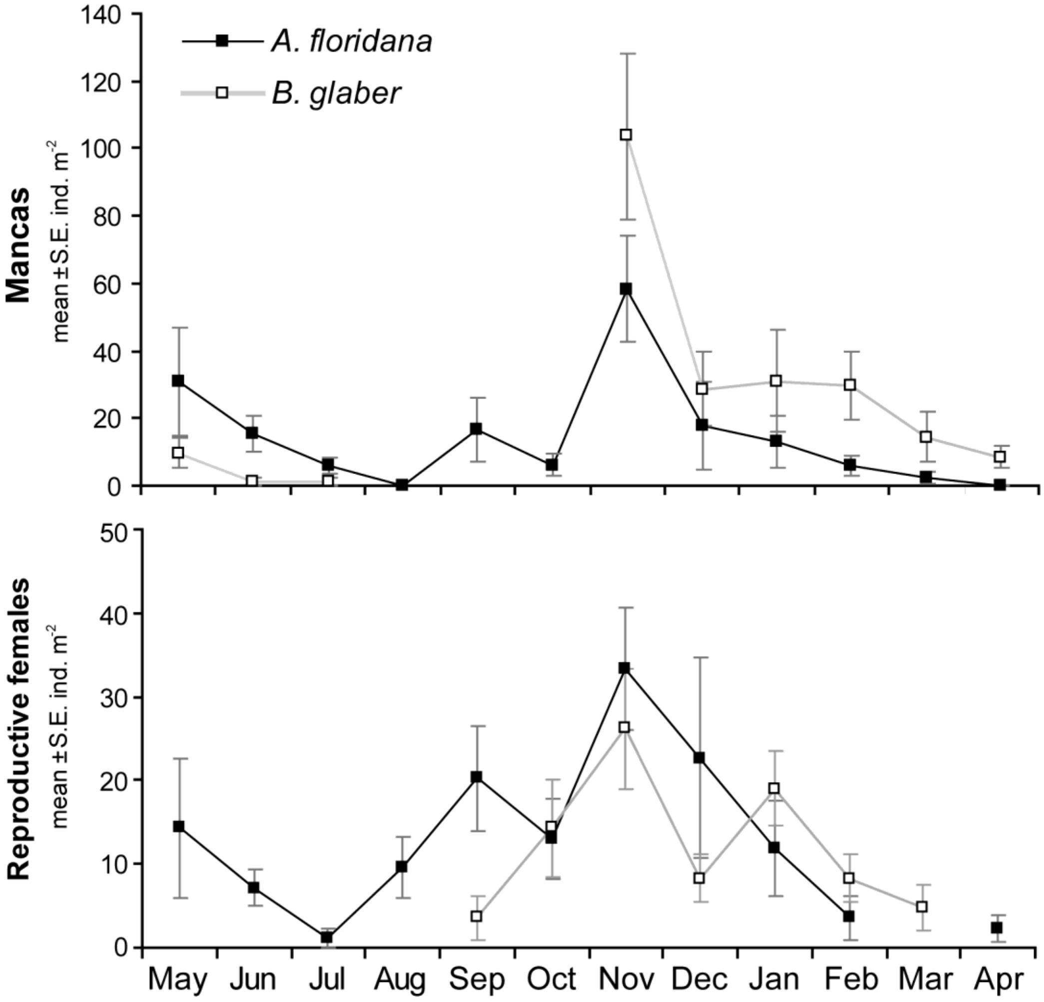
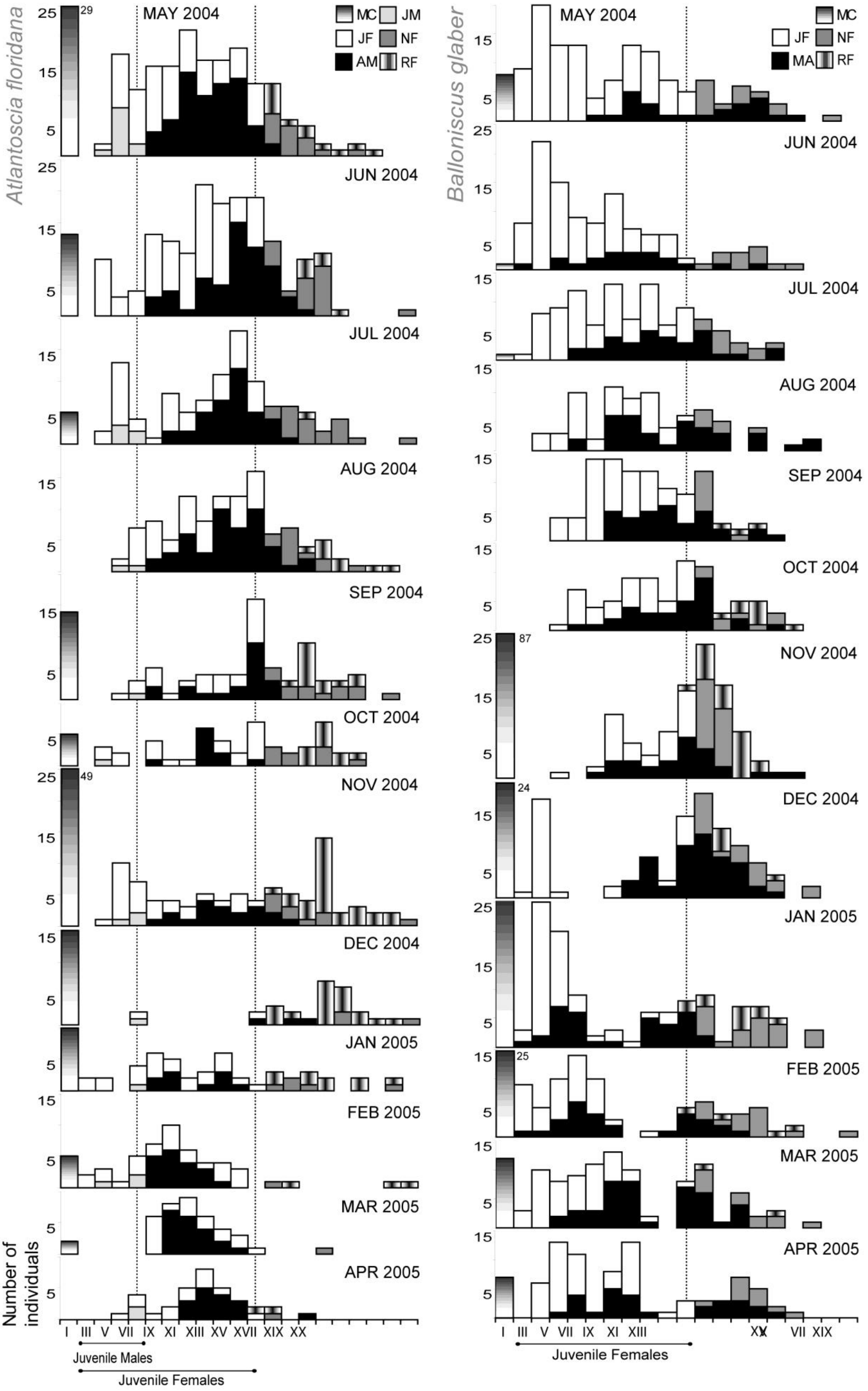


Figure 2. Density of mancas (top) and reproductive females (bottom) of *Atlantoscia floridana* and *Balloniscus glaber*. Values are means ± S.E.

Figure 3. Number of individuals per size class of *Atlantoscia floridana* and *Balloniscus glaber*. The ranges and estimated age of each size class is listed in Table 1. Class I represents the mancas, and the vertical (dotted) lines indicate juvenile size span of males (in the case of *A. floridana*) and females (for both species). MC=mancas; JF=juveniles females; JM=juvenile males; NF=non-reproductive females; RF=reproductive females; AM= adult males; MA=males.


Atlantoscia floridana
Balloniscus glaber
MAY 2004
JUN 2004
JUL 2004
AUG 2004
SEP 2004
OCT 2004
NOV 2004
DEC 2004
JAN 2005
FEB 2005
MAR 2005
APR 2005
MC
JM
JF
NF
AM
RF
MA
29
49
87
24
25
Number of individuals
I III V VII IX XI XIII XV XVII XIX XX
I III V VII IX XI XIII XX VII XIX
Juvenile Males
Juvenile Females

Capítulo III

"Life history comparison of two terrestrial isopods in relation to habitat specialization"

Conteúdo

QUADROS, AF; Y CAUBET & PB ARAUJO. 2009. Life history comparison of two terrestrial isopods in relation to habitat specialization. **Acta Oecologica 35**:243-249.

Life history comparison of two terrestrial isopods in relation to habitat specialization

ALINE FERREIRA QUADROS[1], YVES CAUBET[2,3] & PAULA BEATRIZ ARAUJO[1]

1. Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul. Brazil,

2. Université de Poitiers, Laboratoire de Biologie et Génétique des Populations de Crustacés, UFR Sciences Fondamentales & Appliquées, Poitiers, France,

3. CNRS, UMR 6556 LGBPC, Poitiers, France.

Abstract

For many animal species, there is a relationship between life history strategies, as predicted by the *r-K* selection theory, degree of habitat specialization and response to habitat alteration and loss. Here we compare two sympatric woodlice species with contrasting patterns of habitat use and geographical distribution. We predict that *Atlantoscia floridana* (Philosciidae), considered a habitat generalist, would exhibit the *r*-selected traits, whereas *Balloniscus glaber* (Balloniscidae), considered a habitat specialist, should have the *K*-selected traits. We analyzed several life history traits as well as life and fecundity tables using 715 and 842 females of *A. floridana* and *B. glaber*, respectively, from populations living in syntopy in southern Brazil. As predicted, most evaluated traits allow *A. floridana* to be considered an *r*-strategist and *B. glaber* a *K*-strategist: *A. floridana* showed a shorter lifetime, faster development, earlier reproduction, a smaller parental investment, higher net reproductive rate (R_0), a higher growth rate (r) and a shorter generation time (T) in comparison to *B. glaber*. *Atlantoscia floridana* seems to be a successful colonizer with a high reproductive output. These characteristics explain its local abundance, commonness and wide geographical distribution. On the contrary, *B. glaber* has a restricted geographical distribution that is mainly associated with Atlantic forest fragments, a biome threatened by deforestation and replacement by monocultures. Its narrow distribution combined with the *K*-selected traits may confer to this species an increased extinction risk.

Keywords neotropical isopods; Atlantic forest; life tables; reproduction; oniscidea

Introduction

The study of life history strategies integrates physiological, morphological and behavioral traits to explain how organisms allocate finite resources to maintenance, growth and reproduction, under predictable and unpredictable environments. The *r*-*K* concept (Pianka, 1970; 1972) provides a valuable framework for classifying life history traits, in spite of significant criticism (Parry, 1981; Stearns, 1992). It suggests a continuum between two endpoints along which species can be positioned. The *r*- endpoint represents the quantitative extreme, where the optimal strategy is to allocate energy to reproduction and to produce as many offspring as possible. The *K*- endpoint represents the qualitative extreme, where species allocate energy to competition ability and enhanced survival (Pianka, 1970; 1972).

The tendency of a species' strategy towards the *r*- or *K*- endpoint may be related to the degree of habitat specialization, as it characterizes reproductive and growth rates, and ultimately, a species' colonizing ability. Often, habitat specialists show *K*-selected traits while habitat generalists show *r*-selected traits, and this relationship between reproductive strategies and habitat use allows some predictions about a species' tolerance to habitat disturbances (McKinney, 1997; Purvis et al., 2000; Sakai et al., 2001). Anthropogenic disturbances leading to habitat alteration, loss and fragmentation are known to affect habitat specialists more than habitat generalists (Kitahara and Fujii, 1994; McKinney, 1997; Marvier et al., 2004).

From a conservation perspective, it is important to compare the reproductive strategies of sympatric species, especially when specialists coexist with generalist species in threatened habitats. This is the case of two neotropical woodlice species in southern Brazil. *Atlantoscia floridana* (van Name, 1940) (Philosciidae) is a typical leaf litter isopod, and it is very common and abundant in many habitats of natural vegetation, such as forest edges and interiors, grasslands and supra-littoral vegetation, as well as gardens, parks (Lemos de Castro, 1985; Araujo et al., 1996; Lopes et al., 2005) and even in areas polluted by coal residues (LR Podgaiski pers. comm.). *Balloniscus glaber* (Araujo & Zardo, 1995) (Balloniscidae) is found burrowed in the upper moist soil layer of natural forests (Quadros and Araujo, 2007) and especially in fragments of the Atlantic forest (Lopes et al., 2005; Almerão et al., 2006). The Atlantic forest is a threatened neotropical biome, already reduced to 7.6% of its original extent (Morellato and Haddad, 2000). With those differences of habitat use in mind, we consider *B. glaber* as a habitat specialist and *A. floridana* as a habitat generalist, and we investigated whether their life history strategies can be related to the degree of habitat specialization. We predicted that *A. floridana* would show the traits of *r*-selected species, whereas *B. glaber* should have the traits associated with *K*-selected species.

Materials and Methods

2.1. Woodlice reproduction and studied species

Terrestrial isopods are crustaceans that achieved great success in colonizing a variety of terrestrial landscapes (Warburg, 1987). Among several adaptations to the terrestrial life, modifications in the marsupium (a ventral pouch formed by overlapping oostegites that holds the embryos until fully developed) allow reproduction to take place entirely independently of water (Hoese and Jansen, 1989). The marsupial period is the time interval (days) between the appearance of eggs within the marsupium and their hatching. It lasts for three to seven weeks (Warburg, 1994), during which time the mother nourishes the embryos while providing mechanic protection (Hoese and Jansen, 1989). Female fecundity is determined by the number of developing embryos inside the marsupium, which is constrained by female size (Sutton et al., 1984). After hatching, the young are termed "post-marsupial mancas," due to the lack of the seventh pereionite and pair of legs (Holdich et al., 1984; Araujo et al., 2003). This pair becomes functional after three moults and then individuals are termed "juveniles" until maturation (Araujo et al., 2004). Female reproduction usually starts at the age of one year (Sutton et al., 1984; Dias et al., 2005) and isopods may live up to 5 years (Warburg and Cohen, 1992).

Atlantoscia floridana is a small philoscid species (maximum 7 mm in length) that occurs all along the coast of South America (plus a report in Florida, USA) (Lemos de Castro, 1985). Locally, it is often found at high abundances, up to 1040 ind. m^2 (Araujo and Bond-Buckup, 2005; Quadros and Araujo, 2007). *Balloniscus glaber* is a larger isopod (up to 16 mm in length). It occurs only in the eastern and northeastern region of Rio Grande do Sul state, Brazil. As *A. floridana*'s geographical distribution overlaps all of *B. glaber*'s distribution, they are frequently found in sympatry (Araujo et al., 1996; Lopes et al., 2005). Moreover they show a high syntopy, with 88% of their individuals found together (Quadros and Araujo, 2008).

2.2. Study site and isopod sampling

Isopods were sampled in Itapuã State Park, located in southern Brazil (Viamão, Rio Grande do Sul state; 30°22' S 51°02´ W). This park is a natural protected area of 5560 hectares, established to conserve the original ecosystem of the region. The climate is temperate, without a dry season and with a hot summer (Cfa type of Köppen´s classification; Peel et al., 2007). The landscape is characterized by diverse environments, such as sandy beaches in the margins of Patos lagoon and Guaíba Lake, dunes, and granitic hills (Rio Grande do Sul, 1997). The study site was located on a hill slope, covered by secondary, semi-deciduous forest with trees up to 15 meters high (Brack et al., 1998). A site of 216 m^2 (36 x 6 meters) was divided in 12 sectors with 18 quadrats each. Each month, one quadrat in each sector was sorted and sampled using a corer of 30 cm diameter. The corer's content was transferred to a plastic bag and hand searched in the laboratory to extract all isopods. Samplings were carried out monthly from May 2004 (late autumn) to April 2005 (early autumn), totalling 144 samples, and resulting in 715 *A. floridana* females (with 151 mancas and 98 ovigerous females) and 842 *B. glaber* females (with 174 mancas and 52 ovigerous females).

2.3. Laboratory processing

All female specimens were measured (cephalothorax width; 0.01 mm accuracy). The ovigerous females were dissected for fecundity determination (number of eggs inside the marsupium). The number of mancas inside the marsupium was counted and considered separately. Afterwards, the ovigerous and post-ovigerous (with an empty marsupium) females were dried for 72 h at 60°C and weighed. To obtain the size and weight of the offspring at hatching (Manca I), ovigerous females in the latest stage (with intra-marsupial mancas) were hand-picked from the litter layer, carried alive to the laboratory and kept individually in plastic boxes. After hatching, females and their mancas were measured, dried and weighed.

The developmental rate was measured by (1) individual growth rate until first reproduction and by (2) the length of the brooding period. Individual growth rate (IGR) was calculated as IGR (mm month^{-1}) = ((female size at first reproduction (mm) - size at hatch (mm))/age at first reproduction (months)). The marsupial period was estimated by capturing reproductive females in the earlier stage (with eggs) and following them until hatching in the laboratory.

Based on the cephalothorax width, the age (in days) of each female was estimated using the following equations: $CW=1.682(1-e^{-0.00575(t+59.13)})$ in the case of *A. floridana* (Araujo and Bond-Buckup, 2004) and $CW=2.588(1-e^{-0.00301(t+101)})$ in the case of *B. glaber* (Meinhardt et al., 2007), where *CW* stands for cephalothorax width in mm and *t* is the estimated age in days. Age at first reproduction was defined as the estimated age of the smallest reproductive female found during the entire sampling. Female lifetime was assumed as the estimated age of the largest female individual, reproductive or non-reproductive. To estimate which species starts to reproduce earlier, a relative proportion between age at maturity and female lifetime was determined (age at maturity (days)/female estimated lifetime (days) x 100).

The reproductive effort is usually defined as the proportion of surplus energy that is allocated to reproduction (Stearns, 1992), and one of its measures is the reproductive allocation, a proportion between offspring and maternal mass (Pianka, 1972). To quantify reproductive allocation, the following traits were measured: mean fecundity (eggs per female); manca mass (MM) = individual offspring dry mass in mg; brood mass (BM) = (MM x fecundity); female dry mass in mg (FM). The relationship MM/FM gives a gravimetric index of parental investment (Warburg, 1994), and it was calculated for the smallest (i.e., lighter) and larger females (i.e., heavier), representing the parental investment at the beginning and end of the reproductive life, respectively. The relationship BM/FM was calculated for each ovigerous female and compared via ANOVA.

2.4. Life and fecundity tables

As survivorship, reproductive rate and generation time are important components of the *r-K* theory, we estimated these parameters by constructing vertical (static) composite life-tables for females of both species, following the nomenclature of Stearns (1992) and methods described in Carey (1993) and Ebert (1999). All females were grouped into age classes of one month interval (n_x). Class n_0 (individuals with less then 1 month of age) included the number of mancas found in the population plus the number of intra-marsupial mancas (because they were very near to hatching), divided by 2, to account only for females, assuming a 1:1 primary sex ratio (Araujo et al., 2004). The following parameters were calculated: d_x, the probability of dying between age x and age $x+1$, where $d_x = (n_x - n_{x+1})/n_0$; and l_x, the probability of surviving from birth to the beginning of age class x, where $l_x = n_x/n_0$ (Ebert, 1999). For these parameters, the 95% confidence intervals were calculated following Ebert (1999). Mean life expectancy (e_x), which is the mean number of age categories remaining until death for individuals surviving to the beginning of age class x was calculated as $e_x = T_x/l_x$; where $T_x = T_{x-1} - L_{x-1}$; $T_0 = \Sigma L_x$ and $L_x = (l_x+l_{x+1})/2$ (Carey, 1993). To classify the survivorship pattern, the entropy value (H) was calculated as $H = (\Sigma e_x d_x)/e_0$ (Carey, 1993; Fernandes et al., 2003). The entropy serves as a quantitative characterization of the survival pattern (Goldman and Lord, 1986; Carey, 1993); a value of $H = 0$ indicates that all deaths occur at the same age and $H = 1$ indicates that mortality is exponentially declining (Carey, 1993).

Age-specific fecundity rate (m_x) was defined as the average number of eggs inside the marsupium of females in age class x, divided by 2 as explained above. The gross fecundity rate was given by Σm_x. The net reproductive rate (R_0) was then calculated as $R_0 = \Sigma l_x m_x$ and represents the lifetime expectation of female offspring (Ebert, 1999). Generation time (T, in months) was calculated as $T = (\Sigma x l_x m_x)/R_0$ and finally, instantaneous growth rate (r) was calculated as $r \approx ln(R_0)/T$ (Ebert, 1999).

Results

The life history traits of *Atlantoscia floridana* and *Balloniscus glaber* are summarized in Table 1. Both species show a very constant size and mass at hatching. The length of the brooding period of *A. floridana* is almost half that of *B. glaber*. It also grows faster until first reproduction (at 0.16 mm month^{-1}) and starts to reproduce very early, when 4.4 months old, which represents 30% of its lifetime (Table 1). *Balloniscus glaber* has a longer development time and it starts to reproduce later, when 7.5 months old, which represents 44% of its lifetime (Table 1). There was a difference between the ages of the largest (i.e., oldest) female (30.8 months) and the largest reproductive female in the case of *B. glaber* (16.8 months) (Table 1). This was because the largest female individuals in this species were not found in a reproductive state, while in *A. floridana* the largest females were all in a reproductive state.

In spite of large intrinsic differences in body size, *A. floridana* and *B. glaber* have similar fecundity ranges: 4 to 22 and 5 to 20 eggs per female, respectively (Table 1). At maturity, an individual offspring represents 3.8% of a *B. glaber*'s female mass and 2.7% of *A. floridana*'s, and this percentage decreases to ≈1% in the heaviest females of both species. *Balloniscus glaber* also showed the heaviest brood mass, representing 20% of total female mass, which is significantly higher than *A. floridana*'s (16%)(ANOVA $F_{1,72}$=6.8428; p=0.01) (Table 1).

Both species showed a high probability of death (d_x) in the first three age classes, with only 50% of the population surviving to the fourth class (Table 2). During *A. floridana*'s first three reproductive classes, d_x drops to very low probabilities (Table 2, classes 4 to 6). There is subsequently a high mortality rate in class 7 with 10% of population surviving to 8 months of age and only 1% reaching one year of age (Table 2; l_x). The curves also showed that *A. floridana* survivorship to first reproduction is higher (43%; Table 2; class 4) than *B. glaber*'s, as only 22% of the population achieves class 7, when reproduction begins (Table 2). Through the age classes following maturation, *B. glaber*'s d_x is low, with 10% of the population reaching one year and 1 % reaching the age at last reproduction (Table 2, class 16). From Fig. 1 and Fig. 2 it can be seen that both species had type III survivorship curves (higher mortality early in life), which is also confirmed by the high entropy values of *A. floridana* (H=0.76) and *B. glaber* (H=0.92). Life expectancy at age 0 (e_0) is around 4 months for both species, and continues to decrease over time in *A. floridana*, whereas in *B. glaber* there is a increase in life expectancy for individuals that survive the first three age classes.

Balloniscus glaber presented a higher gross fecundity rate (67.6 offspring female^{-1}), but its survivorship to first reproduction was significantly lower than *A. floridana*'s, which resulted in a slightly lower R_0 (Table 2). The longer time to maturity of *B. glaber* resulted in a longer generation time (T = 10.1 months) and therefore a lower population growth rate ($r \approx$ 0.18 month^{-1}), as expected for the *K*-strategists (Table 2). *A. floridana* showed a lower gross fecundity rate (53.2 offspring female^{-1}), however a higher R_0, a high r and a short T, as predicted for *r*-strategists. Both species showed an increase in m_x with age (Table 2) while $l_x m_x$ decreases (Fig. 3). The highest age-specific contribution to natality of *A. floridana* ($l_x m_x$) is noticed in these three classes and decreases abruptly after the first four reproductive age classes (Fig. 3). Interestingly, at age 15, this species presented a very high fecundity (m_{15}=11), but survivorship to this class was so low (0.006) that a change in m_x produces no changes in the R_0, T or r parameters (data not shown). The *B. glaber* age-specific contribution to natality also decreases with age, but older females continue to provide a significant contribution (Fig. 3).

Discussion

Sutton et al. (1984) were the first to observe an association between the range of habitats occupied by terrestrial isopods and their life history traits (the intrinsic rates of natural increase r, in this case). They recognized the existence of two groups: eurydynamic and steneodynamic species. The eurydynamic species were more surface-active isopods with a higher potential to increase in density, whereas steneodynamic species were those with narrow r ranges and with a habitat mostly restricted to the humus layer of the soil. Accordingly, *A. floridana*, a surface-active isopod which we consider a habitat generalist, showed a set of characteristics corresponding to those of the *r*-strategists: a shorter life span, faster development, earlier reproduction and a reproductive allocation to maximize brood size. These traits in combination result in a lower generation time and high r. In comparison, *B. glaber*, considered here as a habitat specialist, displayed opposite trends and fits well with the expected characteristics of a *K*-strategist. Our results reinforce the Sutton et al. (1984) observation by showing that *A. floridana* and *B. glaber* have opposite life history traits that correspond to their degree of habitat specialization: the eurydynamic species corresponds to a *r*-selected habitat generalist, and the steneodynamic species to a *K*-selected habitat specialist.

A main feature of the *r-K* concept is the existence of a continuum and, quoting Pianka (1970), "certainly, no organism is completely *r*-selected or completely *K*-selected, but all must reach some compromise between the two extremes." As such, not all traits studied here fit with the predictions, and this will be discussed in more detail.

Both survivorship curves derived from the life tables corresponded to Type III, i.e., increased mortality early in life (Begon et al., 2005). Although this does not fit with the predictions for the *K*-strategists, terrestrial isopods are generally expected to suffer a high mortality in the first months (Hassal and Dangerfield, 1990) and in the first year of life (Dias et al., 2005).

Although *r*-strategists are expected to be semelparous and *K*-strategists, iteroparous (Pianka, 1972), both species studied here are iteroparous. However, this prediction is derived from the idea that in a unsaturated environment (*r*-selection), all surplus energy can be invested in reproduction and partitioned into as many offspring as possible (Pianka, 1970; 1972), often culminating in a "big-bang" reproductive event (Pianka, 1976) that leaves no resources for growth and results in senescence, i.e. semelparity. In the case of terrestrial isopods that carry young until they are fully developed, the female body size offers a physical limitation for the number of offspring that can be produced each time. Therefore, for small-bodied oniscidean species, a strategy to produce many offspring is to have several reproductive events, intercalated (or not) with growth events (moults) - the indeterminate growth. *Atlantoscia floridana* clearly adopts this strategy, as it has a faster development, the brooding period is shorter and its reproduction is not constrained to a specific season (Araujo and Bond-Buckup, 2005; Quadros and Araujo, 2007). In view of this, we suggest that the semelparity strategy is replaced by a high degree of iteroparity in this *r*-strategist.

Reproductive effort, here accessed by the reproductive allocation, is predicted to be lower in *K*-strategists, because in a saturated environment (*K*-selection), a greater amount of energy is needed to increase competition ability and to enhance survival (Pianka, 1970; 1972). Even though *B. glaber* showed a higher reproductive allocation, we believe that *B. glaber* invests more in individual offspring (*K*-strategy) rather than in brood size (*r*-strategy) because individual offspring are relatively heavy and fecundity is much lower when compared to isopod species of similar size (Quadros et al., 2008). For example, *Balloniscus sellowii* (Brandt, 1833), a closely related species of similar body size, may bear up to 37 eggs (Quadros et al., 2008) and *Porcellio scaber* (Latreille, 1804) (Porcellionidae), may carry up to 100 eggs (Sutton et al., 1984).

The association between reproductive strategies and habitat specialization has important consequences for species conservation. Habitat generalists have a good colonizing ability and increased tolerance to habitat disturbances (Kitahara et al., 2000; Krauss et al., 2003). Invasive species are commonly habitat generalists with *r*-selected traits (Sakai et al., 2001; McMahon, 2002; Marvier et al., 2004). Habitat specialists, on the other hand, often have low dispersal abilities and have been shown to be particularly affected by disturbances such as habitat fragmentation and loss (Kotze and O´Hara, 2003; Krauss et al., 2003). This occurs because an enhanced competitive ability demands energy and leads to low reproductive rates, delayed maturation and low growth rates (Caley and Munday, 2003), which characterize *K*-selected species (Pianka, 1970; 1972). This trade-off partially explains why specialist species are locally abundant and stable; however, as they usually have a limited geographic range, they experience increased extinction risks (Purvis et al., 2000). *Balloniscus glaber* has local populations with a high density of individuals (up to 500 ind. m^{-2}) with little variation through the year, even when facing a harsh summer that significantly depressed *A. floridana*'s abundance (Quadros and Araujo, 2007). *Balloniscus glaber*'s burrowing ability may protect against desiccation and predation, yet at the same time restricts this isopod to areas of moist, soft soil. In the south of Brazil, most reports of *B. glaber* occurrences are related to Atlantic forest fragments, which are subject to constant deforestation, fragmentation, extrativism and replacement by monocultures (Morellato and

Haddad, 2000). These populations may have an inferior ability to colonize new habitats or to maintain their populations after major habitat losses, in comparison with *A. floridana*, which is a habitat generalist that shows all the elements attributed to a successful colonizer and pioneer species, such as rapid growth, early reproduction, and strong investment in fecundity.

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Table 1. Life history traits of terrestrial isopods (Oniscidea) in Parque Estadual de Itapuã, RS, Brazil. Size refers to cephalothorax width. Means are followed by ±95% confidence intervals. Comparisons were made with ANOVA (* $p<0.05$; ** $p\leq0.01$; *** $p<0.001$). Source: A. Araujo et al. (2004).

Life history traits (Measured by)	*Atlantoscia floridana* PHILOSCIIDAE	*Balloniscus glaber* BALLONISCIDAE
Body size and mass		
Offspring size	0.42 ± 0.01 mm^{A}	0.64 ± 0.01 mm (n=45)
Offspring dry mass	0.05 mg (n=20)	0.15 mg (n=31)
Size of the largest female	1.60 mm	2.47 mm
Heaviest female	4.8 mg	15.3 mg
Developmental rate		
Growth rate until maturity	0.16 mm month^{-1}	0.13 month^{-1}
Length of brooding period	23 days (at 20°C)^{A}	≈40 days (at 23°C)
First reproduction		
Female mass	2.1 mg	3.9 mg
Female size	1.12 mm	1.62 mm
Female estimated age	4.4 months	7.5 months
Onset of first reproduction	30% of female lifetime	44% of female lifetime
Survival to first reproduction		
l_x parameter from life-table	43 ± 7.9 %	21 ± 6.0 %
Lifetime (estimated age)		
Largest female	15.5 months	30.8 months
Age at last reproduction	15.5 months	16.8 months
Reproductive allocation		
Mean fecundity	9 ± 0.6 eggs female^{-1} ***	13 ±1.2 eggs female^{-1} ***
Fecundity range	4 to 22 eggs female^{-1}	5 to 20 eggs female^{-1}
Brood mass/female mass	16 ±1.3 % *	20 ± 3.0 % *
Manca mass/female mass	1.04 – 2.70 % (min-max)	0.90 – 3.80 % (min-max)

Table 2. Life table parameters estimated from field data for terrestrial isopod populations at Parque Estadual de Itapuã, RS, Brazil. Age (*x*) is given in months; n_x = number of females alive in age class *x*; d_x = probability of dying between age *x* and age *x+1* (± 95% confidence intervals); l_x = probability of surviving from birth to the beginning of age class *x* (± 95% confidence intervals); m_x = age-specific fecundity rate; R_0 = net reproductive rate per generation; *T* = generation time; *r* = instantaneous growth rate.

Atlantoscia floridana					*Ballonicus glaber*				
x	n_x	d_x	l_x	m_x	x	n_x	d_x	l_x	m_x
0	151	0.18±0.06	1.00	-	0	174	0.14±0.05	1.00	-
1	124	0.20±0.06	0.82±0.06	-	1	150	0.24±0.06	0.86±0.05	-
2	94	0.11±0.05	0.62±0.07	-	2	108	0.18±0.06	0.62±0.07	-
3	78	0.09±0.04	0.52±0.08	-	3	76	0.10±0.04	0.43±0.07	-
4	65	0.05±0.04	0.43±0.08	2.75	4	60	0.09±0.04	0.34±0.07	-
5	57	0.02±0.02	0.38±0.08	3.81	5	44	0.03±0.03	0.25±0.06	-
6	54	0.07±0.04	0.36±0.08	3.56	6	38	0.00±0.00	0.22±0.06	-
7	44	0.18±0.06	0.29±0.07	4.67	7	38	0.01±0.02	0.22±0.06	4.17
8	16	0.02±0.02	0.10±0.05	5.65	8	36	0.01±0.01	0.21±0.06	4.75
9	13	0.05±0.03	0.09±0.04	4.93	9	35	0.09±0.04	0.20±0.06	6.04
10	6	0.00	0.04±0.03	5.90	10	20	0.01±0.02	0.11±0.05	6.56
11	6	0.03±0.03	0.04±0.03	5.75	11	18	0.00	0.10±0.04	5.80
12	2	0.00	0.01±0.02	5.00	12	18	0.06±0.03	0.10±0.04	8.50
13	2	0.00	0.01±0.02	0.00	13	8	0.00	0.05±0.03	8.40
14	2	0.00	0.01±0.02	0.00	14	8	0.02±0.02	0.05±0.03	6.75
15	1	0.01±0.01	0.006	11.0	15	5	0.01±0.02	0.03±0.02	7.00
					16	3	0.01±0.02	0.02±0.02	9.67
					17	1	0.00	0.006±0.01	-
					18	1	0.00	0.006±0.01	-
					19	1	0.01±0.01	0.006±0.01	-

Atlantoscia floridana	***Ballonicus glaber***
R_0 = 6.9 offspring female^{-1}	R_0 = 6.4 offspring female^{-1}
T = 6.5 months	*T* = 10.1 months
$r \approx$ 0.30 month^{-1}	$r \approx$ 0.18 month^{-1}

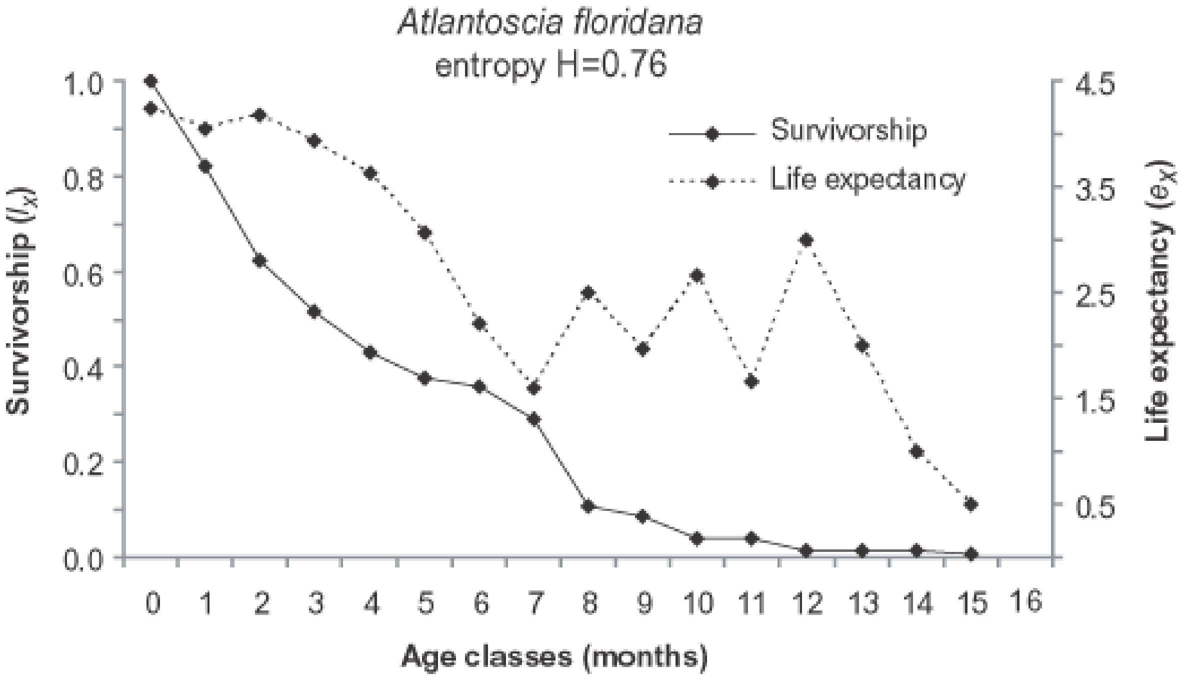

Figure 1. Survivorship curve (l_x), life expectancy (e_x; months) and entropy value (*H*) of *Atlantoscia floridana* (Philosciidae) in Parque Estadual de Itapuã, RS, Brazil, captured from May 2004 to April 2005.

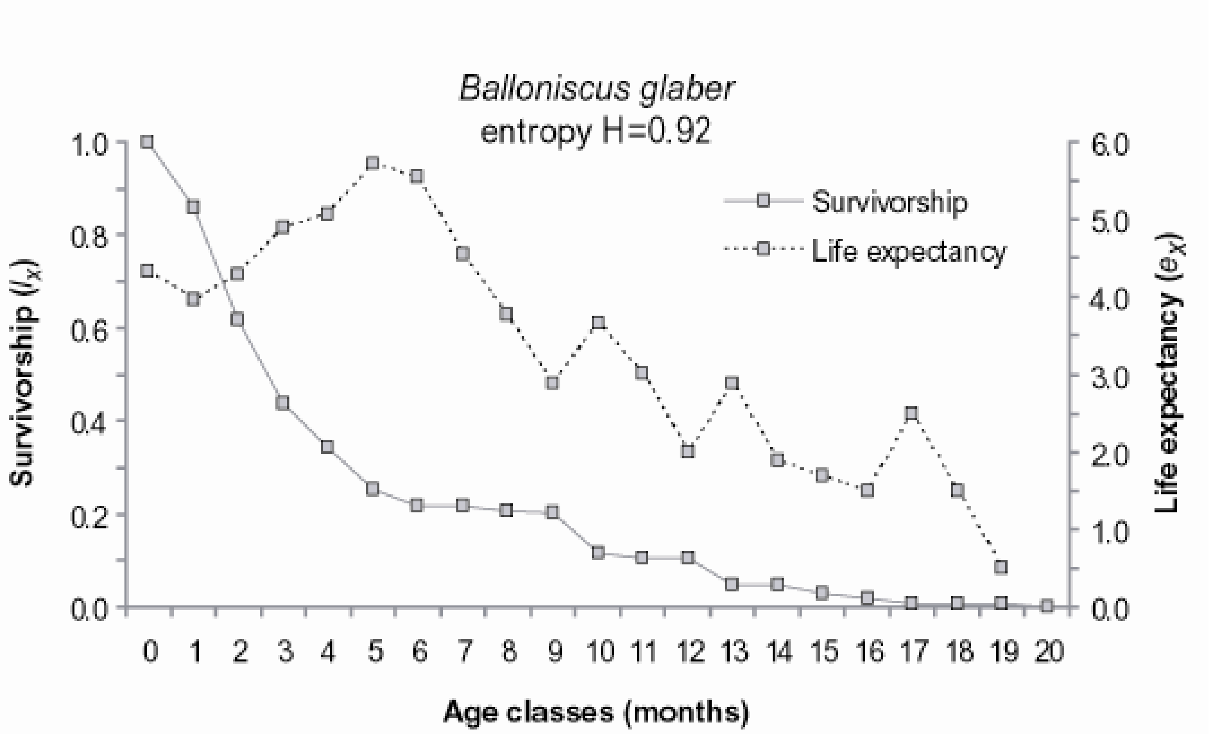

Figure 2. Survivorship curve (l_x), life expectancy (e_x; months) and entropy value (H) of *Balloniscus glaber* (Balloniscidae) in Parque Estadual de Itapuã, RS, Brazil, captured from May 2004 to April 2005.

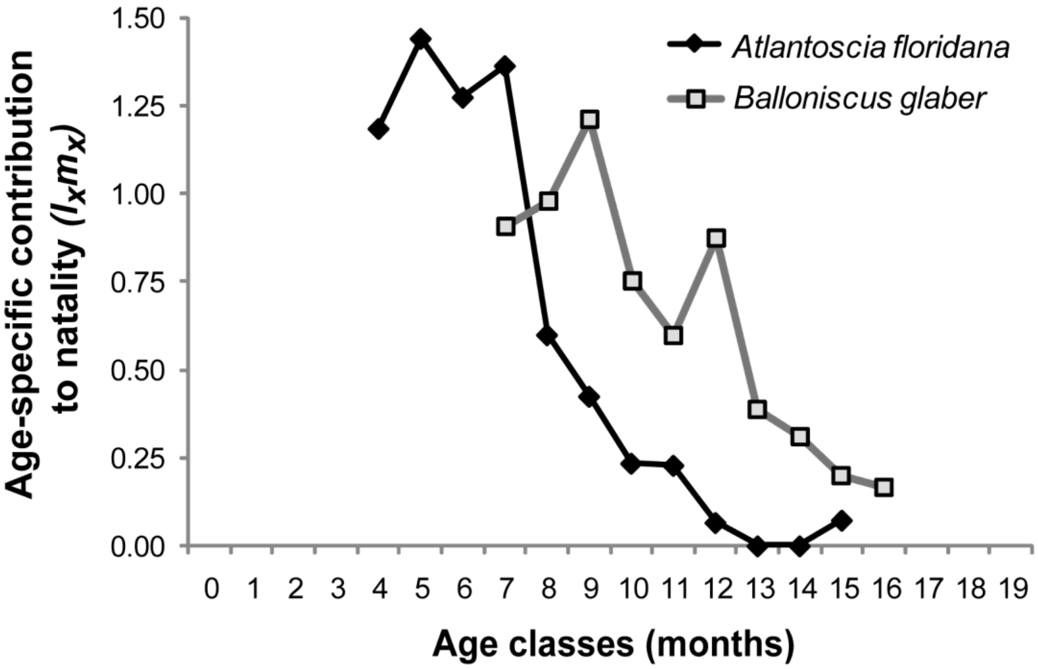

Figure 3. Age-specific contribution to natality ($l_x m_x$) of *Atlantoscia floridana* and *Balloniscus glaber* in Parque Estadual de Itapuã, RS, Brazil, captured from May 2004 to April 2005.

Capítulo IV

"Activity patterns of two syntopic woodlice (Crustacea, Oniscidea)"

Conteúdo

QUADROS AF & PB ARAUJO. Activity patterns of two syntopic woodlice (Crustacea, Oniscidea). Artigo formatado de acordo com as normas do ***Journal of Insect Behavior***.

Activity patterns of two syntopic woodlice (Crustacea, Oniscidea)

ALINE FERREIRA QUADROS[1] AND PAULA BEATRIZ ARAUJO[1]

1. Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul. Porto Alegre, Brazil.

Corresponding Address:

Aline F Quadros - Universidade Federal do Rio Grande do Sul - Departamento de Zoologia. Av. Bento Gonçalves 9500 prédio 43435, CEP 91501-970, Bairro Agronomia, Porto Alegre, RS, Brazil. Phone: +55 51 33087698. FAX: +55 51 33087696. E-mail: quadros.af@gmail.com.

Running head Woodlice activity pattern

Abstract

The dial activity patterns of two syntopic terrestrial isopods from Brazil were investigated. We compared the activity of *Atlantoscia floridana* (van Name, 1940) (Philosciidae) and *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae) in relation to differences in susceptibility to desiccation, influence of heterospecifics in behavior, frequency of activities and choice of habitats for resting. Coexistence of these two species does not seem to influence activity. Circular statistics showed that *Balloniscus glaber* has a higher activity during the night period (from 0000 to 0600). *Atlantoscia floridana* has a highly variable activity pattern, not restricted to the dark phase. Due to this variability, its activity mostly overlaps *B. glaber*'s, and we rejected the possibility of time partitioning. Instead, habitat partitioning through differences in shelter behavior may contribute to decrease species' niche overlap.

Keywords terrestrial isopods; time partitioning; dial cycles; sheltering behavior

Introduction

Terrestrial isopods, or woodlice, are litter or soil inhabitant crustaceans that show a number of remarkable behavioral adaptations to the terrestrial life (Warburg, 1968). Most information available on the behavior of terrestrial isopods concerns the social desert species *Hemilepistus reaumuri* (Milne-Edwards, 1840) (Linsenmair, 2007). This species forms monogamous pairs and close family systems (Linsenmair, 1984) and each family inhabit a burrow that provides better microclimatic conditions (Hoffmann, 1983). These burrows are actively defended against conspecifics and other intruders (Linsenmair, 2007). *Hemilepistus reaumurii* has a crepuscular activity pattern, with distinct dawn and dusk peaks, regulated endogenously (Ammar and Morgan, 2005) and it relies on a well-developed orientation ability to re-locate its burrow after foraging (Hoffmann, 1983).

The behavioral pattern of the desert isopods, however, constitutes a derived pattern among the woodlice and therefore do not correspond to the behavior of most of the 3637 oniscid species (Schmallfuss, 2003) which are not social. During their activity periods the isopods search for food, which they locate through chemoreception (Zimmer *et al.*, 1996). In addition, during exploitation of the habitat the animals must find suitable places to rest (Hassall and Tuck, 2007). The activity pattern of some common leaf-litter woodlice was addressed in the earlier works of Cloudsley-Thompson (1952; 1956), den Boer (1961) and Paris (1963). Their findings indicate that the mechanism controlling the daily activity of the woodlice is exogenous (as a direct response to the environment) rather than endogenous. Cloudsley-Thompson (1952) regarded the photoperiod as the main regulator of *Oniscus asellus* Linnaeus, 1758 activity in the field, this species being essentially nocturnal. Den Boer (1961) and Paris (1963) indicated that moisture also influences the locomotory activity of woodlice. Smith and Larimer (1979) and Refinetti (2000) showed that *Armadillidium vulgare* (Latreille, 1804) has an endogenous circadian clock but it has a weak expression in the locomotor activity and that daily rhythms are determined mostly by inhibition of activity by light (Refinetti, 2000). Other studies indicate that both photoperiod and a species' susceptibility to desiccation interact to determine a species activity period. Species more prone to desiccation, as *Philoscia muscorum* (Scopoli, 1763) (Edney, 1951) have stronger photonegative reactions and are active only during the dark phase, where moisture is higher (Cloudsley-Thompson, 1956). On the other hand, species more tolerant to desiccation such as *A. vulgare* may split its activity along the light and dark phases (Cloudsley-Thompson, 1956; Warburg, 1965). Similarly, Tuf and Jeřábková (2008) showed that *Protracheoniscus politus* (C.L. Koch, 1841) was more active during mornings and twilights while *Porcellium conspersum* (C.L. Koch, 1841) showed an essential diurnal activity, and explain these differences based on the species' resistance to desiccation.

Besides abiotic factors, interactions with other organisms also contribute to the establishment of activity patterns (Kronfeld-Schor and Dayan, 2003). Interactions such as predation and competition influence the timing of activities and the amount of time that is allocated to the different activities that the animals perform along the day. The presence of predators, for example, may increase the time animals spent sheltered (Huang and Sih, 1990) and may cause shifts in the activity periods (Ziv *et al.*, 1993). The presence as well as the density of conspecifics and heterospecifics may also affect key animal activities, such as the time spent foraging (Hassall *et al.*, 2005). Considering sympatric species that are subject to competition, the study of the activity patterns may help to elucidate the mechanisms allowing or facilitating coexistence. In a dial scale, differences in the activity periods decrease niche overlap and facilitate habitat and food partitioning (Carothers and Jaksic, 1984) and may also decrease interference competition by diminishing the frequency of direct encounters of individuals (Kronfeld-Schor and Dayan, 2003; Jaramilo *et al.*, 2003). The high density of individuals of different coexistent species and a high similarity in food preferences are characteristics that may lead both to exploitation and interference competition in assemblages of terrestrial isopods. Ganter (1984) observed that isopods interact and that these interactions decrease growth, survival and reproduction. Hassall *et al.* (2005) showed that *A. vulgare* spent less time feeding on sites of high-quality food when in high-density situations.

In this study we observe the distribution and frequency of activities of two sympatric woodlice in a circadian scale. The neotropical species *Atlantoscia floridana* (van Name, 1940) (Philosciidae) and *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae) occur in abundance inside forests in the south of Brazil (Lopes *et al.*, 2005). These species have high similarity in resource use, showing high intra- and interespecific aggregation levels (Quadros and Araujo 2007; 2008). Besides, they show the same ranking of food preferences (Quadros, unpubl. data). In situations like this, favoring interference and exploitation competition, partitioning of time may have an important role facilitating coexistence. On the other hand, the species seems to differ in their sheltering behavior (Quadros and Araujo, 2007). We attempt to relate their activity patterns to the known relationships of woodlice behavior to biotic and abiotic factors, addressing the following questions: (1) The species differ in their activity periods? (2) Is the period of activity related to a species' susceptibility to desiccation? (3) The presence of heterospecifics influences the timing of the activities? (4) The species differ in their frequency of activities and choice of habitats for resting?

Methods

Laboratory procedures

Adult males and females *Atlantoscia floridana* and *Balloniscus glaber* (henceforth *Atlantoscia* and *Balloniscus*) were hand-searched in the soil and litter layer in a forest fragment inside the Campus of the Universidade Federal do Rio Grande do Sul (30°04'10''S; 51°07'15''W), at Porto Alegre, RS, Brazil, in July 2006. In the laboratory, the animals were sorted by species and sex and ovigerous females and moulting individuals were excluded. Until experimentation, the individuals were maintained in glass containers provided of food and soil from the same sampling site.

Petri dishes of 150 mm diameter were used as experimental units for the observations. They were lined with a layer of plaster to provide homogeneous moisture, and "divided" into three different sectors (Fig. 1). One third of each dish was covered with ≈20 g of soil, previously dried (60 °C, 72 h) and sieved in a 1 mm mesh. Two shelters made of opaque black plastic were placed in the second third. The food consisted of decayed leaf discs (9 mm diameter), sliced into 4 pieces and placed in the remaining section (Fig. 1). This set-up was necessary to distinguish clearly the behavioral acts performed by individuals, which was especially difficult in the case of the small *Atlantoscia* males (less than 5 mm length).

Behavioral acts

A 24-hour observation study was conducted to qualify and categorize the behavioral acts performed by the isopods. For this observation, 30 individuals of each species were distributed into experimental units, totaling five replicates of three males and three females each. Each unit was observed for one minute at every one hour, during 24 hours, totaling 120 minutes of observation per species. The behaviors of the isopods were then divided into two categories of resting states, depending on the substrate the individuals used during inactivity ("In burrows" or "In shelters") and six activity categories (Table I). With the exception of Digging, which was performed exclusively by *Balloniscus*, all behavioral acts listed were performed by both species.

Experimental procedures and observations

The frequency of activities was quantified in an experimental design similar as described above. Twenty-seven individuals of each species were distributed into experimental units to form three replicates containing three males and three females of *Atlantoscia*, another three replicates with *Balloniscus* (single-set experiment) and three replicates containing three individuals of each species (mixed-set experiment). There was a period of 72 hours of acclimation before the start of the observation sessions.

The observation sessions were conducted at every two hours (even hours), along 24 hours. In each session it was determinate the number of individuals resting, in burrows or in shelters. Then, for five minutes it was recorded all behavioral acts performed by the individuals that were active ("all occurrences" method sensu Altmann, 1974). The first observation occurred three days after the start of the experiment; the second observation was made after five days and the third, after seven days. In between, the animals were left undisturbed.

The observations were conducted in a quiet room, subject to natural photoperiod and temperature. By the time this experiment was conducted, in winter, sunrise occurred around 07:30 and the sunset around 17:30, corresponding to a 10:14 L:D hour regime. Mean temperature was 19°C. During the night, observation was made with fluorescent lamps covered by red cellophane sheets (Pereira *et al.*, 2004). The petri dishes were moisturized at every six hours with a water sprayer.

Analyses

To investigate whether the woodlice differ in their activity periods, we utilized a circular statistics analyses to examine the distribution of the activities along the day. The sum of all behavioral acts performed in each session was used as a measure of the activity level. Then, the activity levels were tested for non-random distribution using Rayleigh's z-test. Rayleigh's z-test for circular data was performed using the software package Oriana (Kovach, 1994). To investigate whether the presence of heterospecifics influences the timing of the activities, these analyses were also applied to the data of the mixed-set experiments.

A repeated measures ANOVA was employed to compare the activity levels (number of behavioral acts per session) of the two species in the single-set treatments, where the sessions were treated as the repeated factor. The frequency of the activities performed by the isopods was compared with a T-test. To verify if each species showed a preference for the two habitat types available for shelters, a T-test was also employed, comparing the average percentage of individuals resting in burrows and in shelters along the observation sessions. Percentage and frequency data were arc-sine transformed prior to the analysis to ensure homocedasticity (Underwood, 1997).

Results

In the first observation, which occurred three days after the settlement of the animals in the experiment, the analysis of circular data showed that *Atlantoscia* had a random activity pattern (Table II; Fig 2A). During the next two observations its activity became less variable and more concentrated in the evening and beginning of night and the Rayleigh's z-test confirm its unimodality (Table II; Fig 2A). *Balloniscus* showed a clear peak of activity in the sessions before dawn, from 03:00 to 05:00, both in the 1st and 3rd observations (Table II; Fig. 2B). In the second observation, activity was variable along the 24-hour cycle (Table II; Fig. 2B). Comparing the length of the mean vectors in the different observations, it could be noted that the activity of *Atlantoscia* is in most cases highly variable and results in low values of *r* while the activity pattern of *Balloniscus* is more consistent and shows satisfactory *r* values (Tables II, III).

In the mixed-set experiments, the activity pattern of *Atlantoscia* was also highly variable, with no well-defined activity period in the 1st and 3rd observations (Table III; Fig 3A). Only in the second observation its activity was significantly unimodal, with a mean vector at 01:04 and a length of 0.45 (Table III). Again, the activity pattern of *Balloniscus* was more consistent, concentrated in the night, with mean vectors at 01:00 to 03:00 and very high *r* values (Table III; Fig. 3B).

The results of repeated measures ANOVA indicate that the number of behavioral acts per session was not significantly different (mean of 5.21±0.72 acts per session for *Atlantoscia* and 3.87±0.70 acts per session for *Balloniscus*)(Anova $F_{1,16}$= 1.706; p=0.21).

Along the day the activities performed more frequently by *Atlantoscia* were Monitoring and Interaction (Fig. 4A) and by *Balloniscus*, Exploring and Interaction (Fig. 4C). Feeding events occurred along all the 24-hour cycle, as well as Digging in the case of *Balloniscus* (Fig. 4A, 4B). Overall, *Atlantoscia* showed a higher frequency of Monitoring (T test; t=10.437; p<0.0001) and a lower frequency of Cleaning acts (T test; t=2.270; p=0.037)(Fig. 5) as compared to *Balloniscus*. *Balloniscus* showed a much higher percentage of individuals resting (73.6%), in burrows or in shelters along the day, as compared to *Atlantoscia* (39.9%)(T test; t=5.687; p<0.001) (Fig. 4B, 4D). With respect to the habitat chosen for resting, 58.9% of *Balloniscus* individuals were resting in burrows and only 14.6% were resting in shelters (T test; t=3.526; p=0.02). *Atlantoscia* showed no preference for either type (T test; t=1.202; p=0.295).

Discussion

The species' activity pattern comprises the timing and the frequency of the behavioral repertory and provides important clues on how species are influenced by biotic and abiotic factors. Abiotic factors such as the photoperiod causes repetitive changes in the environment that can be anticipated by the animals (Welsh, 1938), allowing the activities to take place whether the environmental conditions are more suitable for them (Hoenen and Gnaspini, 1999). Several studies indicate that woodlice are essentially nocturnal animals, with their activity regulated by the saturation deficit of the atmosphere. Paris (1963) observed that *Armadillidium vulgare* becomes active only when permitted by an atmosphere that will not induce excessive transpiration and that even in the winter the peak of dial activity occurs in the middle of the night, when the saturation deficit of the atmosphere is at its lowest. Accordingly, *Atlantoscia* and *Balloniscus* showed a higher activity during the dark phase of the dial cycle. However, only *Balloniscus* showed a consistent higher activity during the night period in both treatments and in the three observations. *Atlantoscia* showed a much more variable activity, showing peaks in different periods of the day in the different treatments and observations. The observed variation is largely due to intraspecific differences. Ammar and Morgan (2005) also registered intraspecific variability on the activity pattern of *H. reaumurii*. Therefore, *Atlantoscia* and *Balloniscus* activity periods highly overlap in both treatments and there was no indication that partitioning of time takes place between them, at least in the conditions studied here. It is possible that the activity reported here, under a suitable temperature and moisture conditions, corresponds to the maximum activity that these isopods may exhibit. In summer drier conditions, their activity may become less variable and more restricted to the dark phase.

Woodlice loose water during their foraging and exploitation activities and then must search for moist retreats (Kuenen and Nooteboom, 1963). In their moist shelters, they actively absorb water from the air (Wright and Machin, 1990) and meanwhile they digest food protected from predators. Therefore, good shelters are essential to isopods, enabling them to be prepared for the next foraging excursions (Hassall and Tuck, 2007). The differences in sheltering behavior observed during the resting periods corroborate previous findings that *Atlantoscia* is a surface litter species whereas *Balloniscus* has more endogean habits (Quadros and Araujo, 2007; 2008). In the litter layer of the interior of forests, several elements offer a structural variety of shelters for meso- and macrofauna arthropods. Among them, leaves often curl as they dry and form the “curled leaves” or “leaf shelters” (Stevenson and Dindal, 1982). In the field, *Atlantoscia* individuals are often found inside those leaf shelters, which also harbors a great quantity of fecal pellets and indicate that leaves had been long used as shelters (pers. obs.). Hassall *et al.* (2005) suggested that woodlice might compensate for the time they spent sheltering by feeding on the feces that accumulate under the shelters and in accordance, in the present observations a great number of fecal pellets accumulated under the artificial shelters, and both species were seen feeding on them. *Balloniscus* used the artificial shelters less frequently, resting mostly inside the burrows made by themselves or conspecifics. This finding corroborates Araujo and Zardo (1995) and Quadros and Araujo (2008) observations that this species is commonly found burrowed in the occasion of field samplings. This burrowing ability is advantageous because, besides protecting against desiccation, it provides a shelter from predators that do not posses excavatory capabilities, such as spiders and chilopodans (Villani *et al.*, 1999). The higher frequency of cleaning acts, as compared to *Atlantoscia*, is definitely related to *Balloniscus* excavatory behavior.

Based on observed differences in sheltering behavior, intraspecific differences in activity patterns and the absence of aggressive behavior between *Atlantoscia* and *Balloniscus*, we conclude that the species show a high degree of tolerance. If competition is to take place between these species where they coexist, it is more likely to be exploitation competition (for food and not for shelter) rather than interference competition. In spite of a high similarity in food preferences, large differences in the sheltering behavior and intraspecific variability help to decrease their niche overlap.

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Table I. Resting states and behavioral acts of the woodlice *Atlantoscia floridana* (Philosciidae) and *Balloniscus glaber* (Balloniscidae), in laboratory conditions.

Type	Categories	Behavioural acts
Resting States	In burrows (BUR)	Completely hidden within the soil, out of sight;
		Partially burrowed in the soil, sometimes with the head or uropods visible;
	In shelters (SHE)	Standing inside the plastic shelter without movement;
		Standing inside the shelter doing slightly movements;
Activity acts	Monitoring (MON)	Standing still on the surface and outside the shelters, slightly moving the antennae to different directions;
	Exploring (EXP)	Walking around the dish;
		Running around the dish;
		Touching the substrates (soil, dish ground, leaves, plastic shelters) with the antennae;
	Feeding (FEE)	Handling and/or eating leave pieces, soil particles, faecal pellets;
		Defecating;
		Repeatedly touching a substrate with the uropods (drinking);
	Cleaning (CLE)	Using the first pair of pereopods to clean the antennae;
		Using the first pair of pereopods to clean the other pereopods;
	Interacting (INT)	Touching other individual(s) with the antennae;
		Touching other individuals with the pereopods;
		Being in physical contact with another(s) individual(s);
	Digging (DIG) (only *B. glaber*)	Using the pereopods to dig into the soil;

Table II. Results of the circular statistics indicating the periods of highest circadian activity of *Atlantoscia floridana* and *Balloniscus glaber*. Activity peaks are shown for observations conducted after three (1st observation), five (2nd observation) and seven days (3rd observation) after the beginning of the experiment. Values of significance (p) are indicated with asterisks: ** p<0.01; *** p<0.001; NS = non significant.

	1st observation	**2nd observation**	**3rd observation**
	Atlantoscia floridana		
mean vector	14:56	20:15	00:01
(95% c. i.)	(--)	(18:22-22:07)	(09:45-14:17)
Length (*r*)	0.05	0.18	0.18
Rayleigh Test (*z*)	0.650^{ns}	**7.871*****	**5.355****
	Balloniscus glaber		
mean vector	4:05	01:04	05:18
(95% c. i.)	(02:49-05:20)	(--)	(04:27-06:09)
Length (*r*)	0.40	0.13	0.48
Rayleigh Test (*z*)	**16.227*****	3.099^{ns}	**34.041*****

Table III. Results of the circular statistics indicating the periods of highest circadian activity of *Atlantoscia floridana* and *Balloniscus glaber* in the mixed-set experiments. Activity peaks are shown separately for observations conducted after three (1st observation), five (2nd observation) and seven days (3rd observation) after the beginning of the experiment. Values of significance (p) are indicated with asterisks: ** p<0.01; *** p<0.001; NS = non significant.

	1st observation	**2nd observation**	**3rd observation**
Atlantoscia floridana (with presence of *B. glaber*)			
mean vector	10:04	01:26	01:23
(95% c. i.)	(--)	(00:01- 02:51)	(--)
Length (*r*)	0.26	0.45	0.26
Rayleigh Test (*z*)	1.657^{ns}	**12.531*****	2.307^{ns}
Balloniscus glaber (with presence of *A. floridana*)			
mean vector	02:30	01:01	03:23
(95% c. i.)	(00:42 – 04:18)	(00:04 – 01:58)	(02:18 – 04:28)
Length (*r*)	0.40	0.73	0.72
Rayleigh Test (*z*)	**7.964*****	**20.688*****	**16.395*****

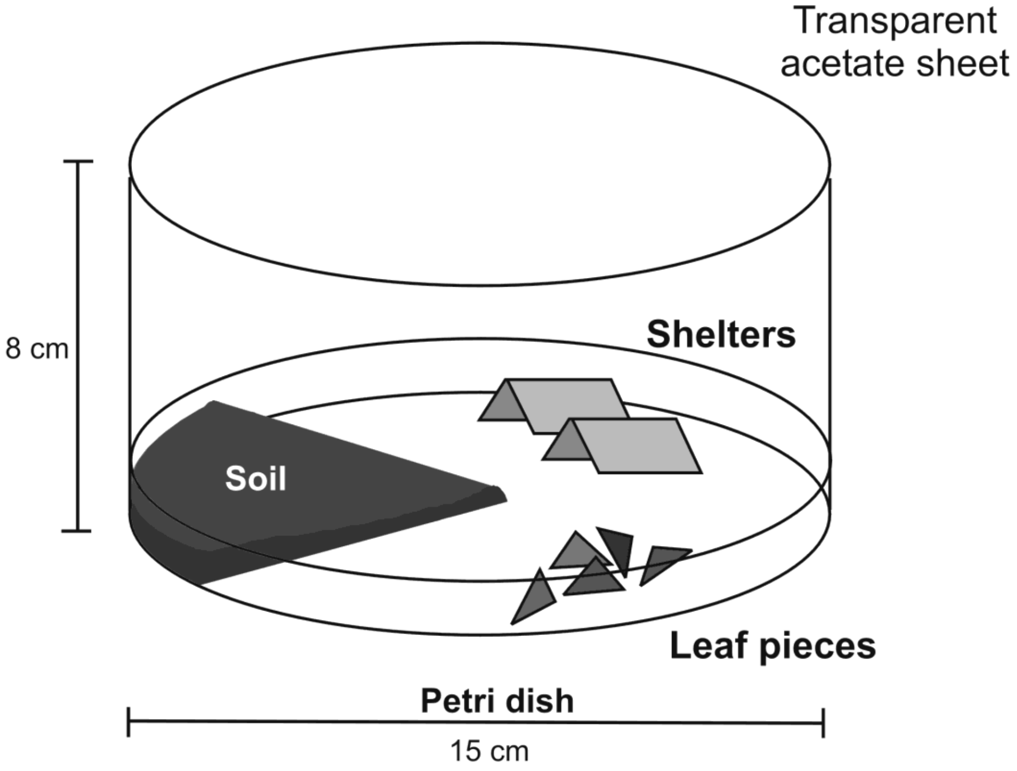
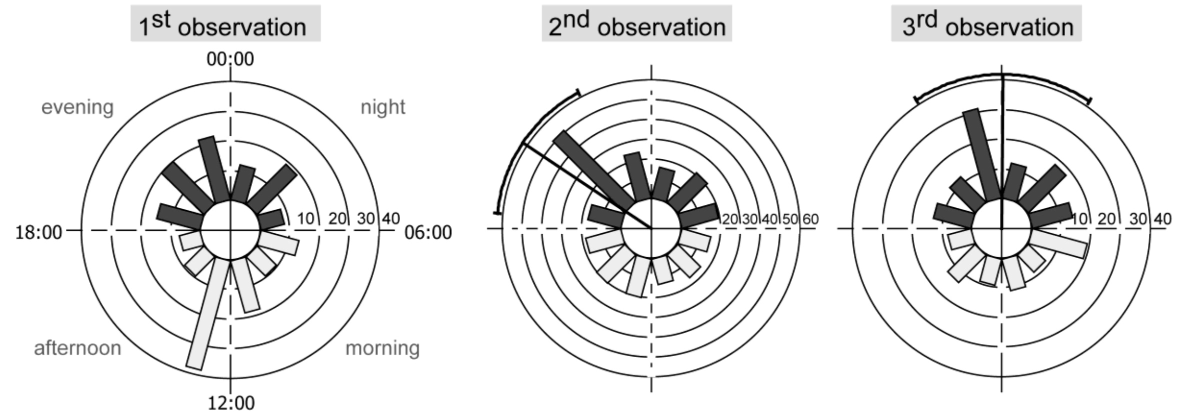
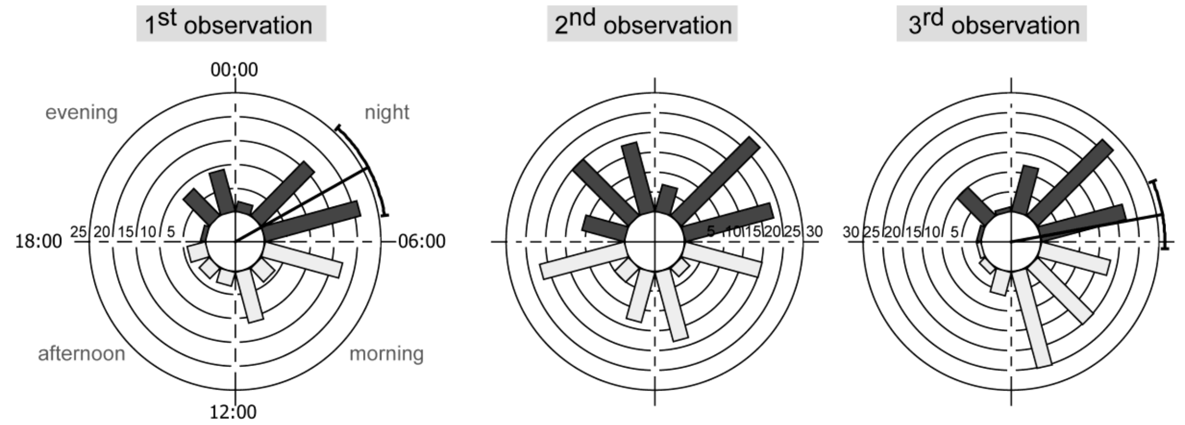


Fig. 1. Illustrative drawing of the experimental units utilized to observe terrestrial isopod behavior. The units were composed by 15 cm diameter Petry dishes, lined with a layer of plaster of paris. A transparent acetate sheet (8 cm height) was fixed around the dish to increase the height of the dish and impede the escape of the animals.



A. *Atlantoscia floridana*



B. *Balloniscus glaber*

Fig. 2. Circadian activity of *Atlantoscia floridana* (A) and *Balloniscus glaber* (B) in the single-set experiments. The circular diagrams show the activity after three (1st obs.), five (2nd obs,) and seven days (3rd obs.) after the beginning of the experiment. The bars represent the frequency of activity acts during daylight (light-grey) and nightlight (dark-grey) sessions; the vectors in black indicate the mean and the 95% confidence intervals. Refer to Table II for details on the circular statistics results.

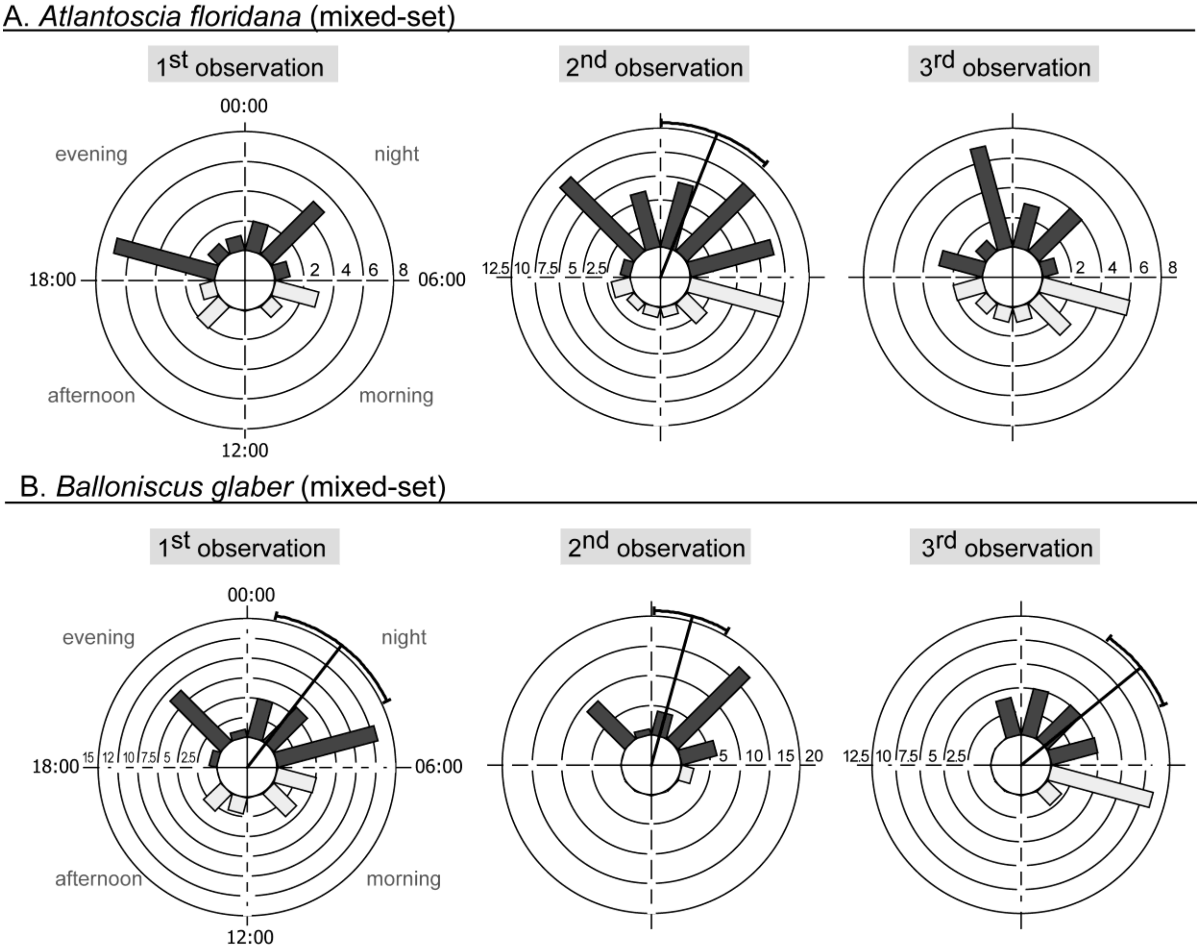


Fig. 3. Circadian activity of *Atlantoscia floridana* (A) and *Balloniscus glaber* (B) in the mixed-set experiments. The diagrams show the activity after three (1st obs.), five (2nd obs,) and seven days (3rd obs.) after the beginning of the experiment. The bars represent the frequency of activity acts during daylight (light-grey) and nightlight (dark-grey) sessions; the vectors in black indicate the mean and the 95% confidence intervals. Refer to Table III for details on the circular statistics results.

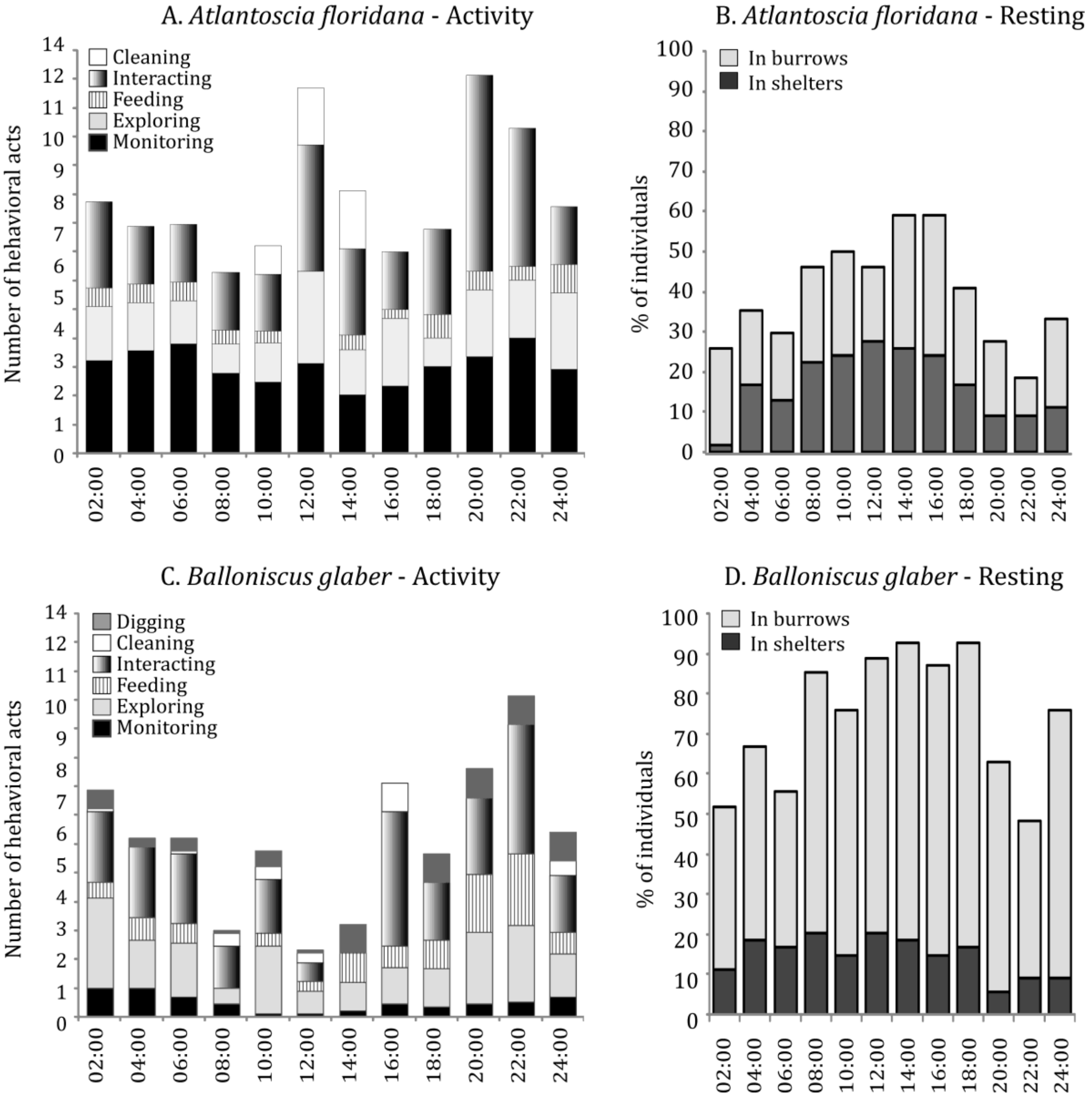


Fig. 4. Circadian activity pattern of Neotropical terrestrial isopods. The different activities performed by the isopods are shown as mean number of behavioral acts per session (A and C). The resting behavior is expressed as mean percentage of individuals resting in each session of observation and the habitat chosen for resting (B and D).

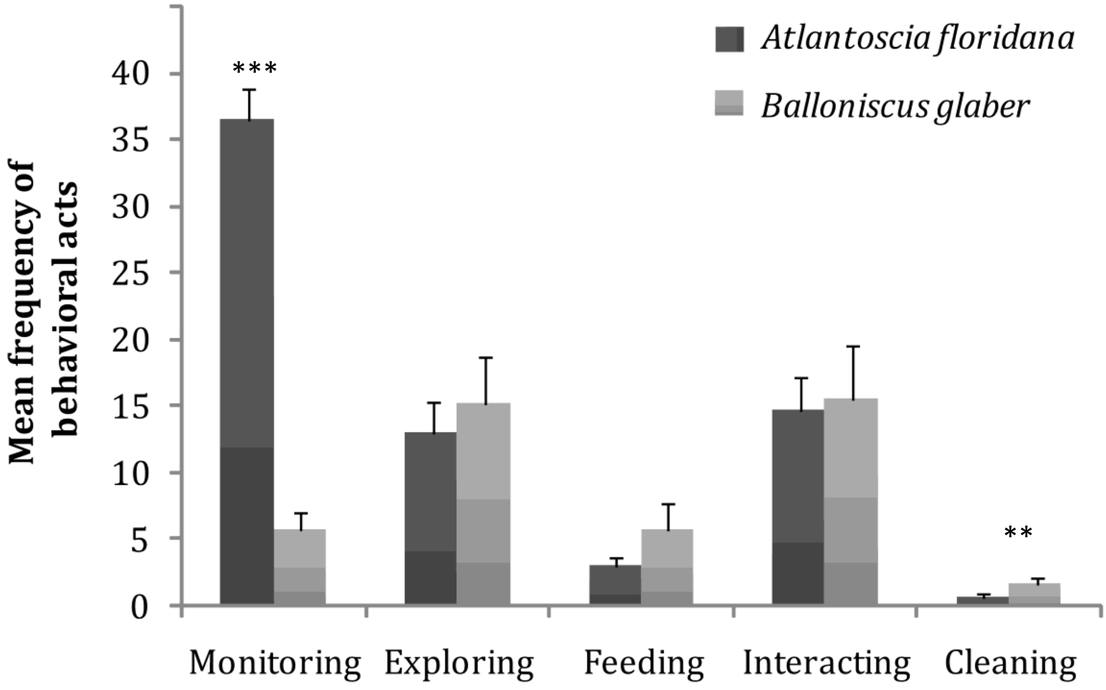


Fig. 5. Frequency of behavioral acts of *Atlantoscia floridana* and *Balloniscus glaber*. Data is shown as mean ± s.e. and the asterisks indicate significant differences between species (t test; *** $p < 0.001$; ** $p < 0.01$).

Capítulo V

"Common feeding preferences of neotropical and paleartic detritivores and their relationship with plant traits"

Conteúdo

QUADROS AF, M ZIMMER, PB ARAUJO & JG KRAY. Common feeding preferences of neotropical and paleartic detritivores and their relationship with plant traits. Artigo formatado de acordo com as normas do periódico ***Functional Ecology.***

Common feeding preferences of neotropical and paleartic detritivores and their relationships with plant traits

ALINE F QUADROS[1], MARTIN ZIMMER[2], PAULA BEATRIZ ARAUJO[1] & JAIR GILBERTO KRAY[3]

1. Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil;

2. Zoologisches Institut, Christian-Albrechts-Universität zu Kiel, Kiel, Germany;

3. Programa de Pós-Graduação em Botânica, Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil;

Corresponding address - Aline F Quadros - Universidade Federal do Rio Grande do Sul - Departamento de Zoologia. Av. Bento Gonçalves 9500 prédio 43435, CEP 91501-970, Bairro Agronomia, Porto Alegre, RS, Brazil. Phone: +55 51 33087698. FAX: +55 51 33087696. E-mail: quadros.af@gmail.com.

Running head Woodlice feeding preferences

Summary

1. On a local scale, litter decomposition rates are governed by litter chemistry and the activity of soil organisms. Detritivores are likely to influence decomposition and nutrient cycling rates directly and indirectly. Their populations are likely to be bottom-up regulated and constrained not only by litter biomass but also by litter chemistry. Therefore, their decisions towards specific leaf litter types for feeding are likely to influence decomposition as well as their population dynamics.

2. We investigate how multiple leaf litter traits combine to determine palatability to detritivores. We offered litter from five neotropical evergreen and five paleartic deciduous trees to two woodlice (Oniscidea, Crinocheta) from the neotropics (*Atlantoscia floridana* and *Balloniscus glaber*) and two paleartic (*Porcellio scaber* and *Philoscia muscorum*), in multi-choice feeding experiments. Plant litter was characterized regarding three classes of traits: structure-related (lignin, cellulose, toughness), nutrient-related (Ca, N, P, lipids) and secondary compounds (amount and activity of total phenolics).

4. Neotropical and paleartic isopods showed the same preferences ranking. Feeding preference increases with the decrease in thickness, C:N ratio, cellulose and phosphorous and increase in nitrogen and calcium content, while consumption rates were positively correlated to carbohydrates and lipids and negatively correlated to cellulose, carbon and fiber.

5. Rejection of food by terrestrial isopods occurs when litter has: (1) high density of trichomes; (2) a combination of toughness >50 g mm^{-2} and C:N ratio >25; or (3) a combination of N <2%, C:N >25 and cellulose >30%. The preferred food is the one with N >2%, Calcium >1%, thickness < 0.1 mm. Among plants that fulfilled these last characteristics, neotropical isopods prefer leaves with C:N ratio <20 and lignin <20% while paleartic isopods showed preferences towards increased phenolic content (>2%).

6. We demonstrated that traits that governs decomposability of litter and vegetation responses to herbivory also determines palatability to detritivores.

Keywords detritivory, leaf traits, litter palatability, nutrient cycling, terrestrial isopods

Introduction

In terrestrial ecosystems, the dynamics of detritus decomposition interplays the soil availability of nutrients and primary production. Especially in forests, where the majority of aboveground plant biomass returns to the soil as detritus and forms the litter layer, understanding the dynamics of detritus composition, accumulation and breakdown is of great importance. The litter layer constitutes a large pool of organic matter in the soil and it is the substrate for the decomposer communities that breaks down organic compounds and mineralize nutrients. Besides its importance to nutrient cycling, the litter layer is a heterogeneous and abundant resource and constitutes habitat and food for the detritus food web (Takeda & Abe 2001; Moore et al. 2004), which harbors the lowest trophic levels and sustain many soil food chains (Moore et al. 2004).

In a given ecosystem, decomposition rates of plant litter determine if there will be an accumulation of large nutrient stocks in a soil surface horizon or if litter will be rapidly degraded, releasing nutrients to producers (Attiwill & Adams 1993; Lavelle 1997). On a global scale, rates of litter decomposition are regulated by climate and within a particular climatic region or ecosystem, the best indicator of decomposition rates is litter chemistry (Knoepp 2000). Litter chemistry in turn is influenced by herbivory and plant resource acquisition strategies (Coley, Bryant & Chapin III 1985; Coley & Barone 1996; Diaz et al. 2004), and thus, depending on the interactions of these factors, plant species from the same ecosystem will differ largely in relation to the litter they produce (Perez-Harguindeguy et al. 2000). The leaf traits that favors high decomposition rates are in general the same traits that increase palatability to herbivores, as for example high N, low C:N ratio and low toughness (Pennings & Paul 1992; Pennings et al. 1998; Cornellissen et al. 1999; Pérez-Harguindeguy et al. 2003). To counteract the action of herbivores, living plants possesses a great array of defenses of their photosynthetic tissues, mainly mechanical, as the production of tough leaves rich in recalcitrant compounds (Pennings et al. 1998) and trichomes, and chemical, as the production of phenolic compounds, alkaloids and terpenes through the secondary metabolism (Schoonhoven, van Loon & Dicke 2005). Many of these compounds are retained after leaf senescence and characterize the resultant leaf litter. If present in high amounts they will slow down decomposition rates (Taylor, Parkinson & Parsons 1989; Perez-Harguindeguy et al. 2000; Wardle, Bonner & Barker 2002), as they turn the litter into a more resistant material, to both the action of abiotic factors and decomposer community (Findlay et al. 1996; Schweitzer et al. 2005). Thus, herbivory and litter chemistry may exert indirect and direct effects, respectively, on soil organisms involved in decomposition, altering the quality of their food sources (Bardgett, Wardle & Yeates 1998). Detritivores, for instance, depend upon plants for their energy resources and play an important role in litter decomposition. They comminute, fragment and transport the litter, increasing its breakdown rate (Bocock 1964; Cárcamo et al. 2001; Morón-Ríos 2008). Also, their activity results in the dissemination of fungal spores and mycelium and in the accumulation of fecal pellets which represent microsites for enhanced microbial activity (Attiwill & Adams 1993; Lavelle 1997; Hassall, Turner & Rands 1987; Zimmer).

While there are many studies relating herbivore preferences to leaf traits (Pérez-Harguindeguy et al. 2003; Pennings et al. 1998) and the relation of plant traits and litter chemistry in decomposition rates (Findlay et al. 1996; Schweitzer et al. 2005), few studies have dealt with the relationship between litter traits and palatability to detritivores and the consequences for ecosystem function. Here we investigate this relationship, using woodlice as model detritivores, because they are spread worldwide and inhabit a variety of ecosystems, often representing a large portion of detritivore biomass (Hassall & Sutton 1977; Zimmer 2003; Gongalsky et al. 2005; Bastow, Preisser & Strong 2008; Quadros & Araujo 2008). Previous works have estimate that they may be responsible for the processing of 2% (Lam, Dudgeon & Ma 1991; tropical forest), 7% (Mocquard et al. 1987; temperate forest), 10% (Dias & Sprung 2003; salt marsh) and 16% (Quadros & Araujo 2008; semideciduous forest) of the annual leaf litter input. More specifically, we address the following questions: (1)

Which traits or combination of traits determine leaf litter palatability to woodlice? (2) Are those the same traits that determine food intake rates? (3) The feeding preferences of neotropical and paleartic woodlice species differ? Based on our results and reviewing the literature, we propose a template for woodlice feeding preferences and discuss it in relation to isopod ecology and consequences to ecosystem functioning.

Material and Methods

Woodlice

Isopod species from the paleartic region were represented by *Porcellio scaber* Latreille, 1804 (Porcellionidae) and *Philoscia muscorum* (Scopoli, 1763) (Philosciidae). These are native to Europe although both species are found outside their native ranges of distribution due to human dispersion: *Porcelio scaber* is distributed worldwide (Schmalfuss 2003), including Brazil (Araujo, Buckup & Bond-Buckup 1996) and *Philoscia muscorum* is introduced in North America (Hornung & Slávecz 2005). They were captured by hand, from under rocks, in the vicinity of Kiel University, Kiel, Germany.

The species *Atlantoscia floridana* (van Name, 1940)(Philosciidae) and *Balloniscus glaber* Araujo & Zardo, 1995 (Balloniscidae) are native to the Neotropical region and very common in forests of the coastal and southern regions of Brazil, respectively (Quadros & Araujo 2007). *Atlantoscia* has the widest distribution and occurs along all the coast of South America and *Balloniscus glaber* occurs in the south of Brazil. Although occasionally found in antropic habitats, these species are common inhabitants of semideciduous and tropical forests in Brazil. Henceforth, isopods will be referred by their generic names.

Study sites and collection of leaf litter

Before accessing the relationships between leaf traits and feeding preferences, it was necessary to characterize the vegetation and leaf litter layer of the study site, in order to know which food types are available to the isopods. For that purpose we chose a forest fragment (semi-deciduous seasonal forest) in Morro Santana nearby the Campus do Vale of the Universidade Federal do Rio Grande do Sul (Porto Alegre city, Rio Grande do Sul, Brazil). This site represents the natural systems inhabited by *Atlantoscia* and *Balloniscus* and it is an abundant source of individuals (Quadros & Araujo 2007, 2008). The vegetation in this site is a secondary forest in advanced stage of regeneration and belongs to the "Mata Atlântica" biome (Consórcio Mata Atlântica & Unicamp 1992). Its flora has influence from the Paraná-Uruguai (estacional forest) basin and also from of the Atlantic pluvial forest (Rambo 1951).

In an area of ≈ 1 hectare, a survey of dicotyledonous arborous plants revealed the occurrence of 48 species (Table 1). To know which species are represented in the leaf litter layer and in which amounts, 40 litter samples were taken randomly with a soil corer of 30 cm diameter. The samples were air dried and weighed. Then, these samples were carefully searched to separate non-decomposed leaves (leaves with an intact lamina, mostly brown, and showing no signs of detritivory) from other leaf litter constituents (decomposed leaves, seeds, barks, roots, loose soil, humus). The total weight of samples averaged 108.7±7.05 g and had a density of 72.2 g m^{-2} of decomposed leaves and 21.7 g m^{-2} of non-decomposed leaves. The fraction of non-decomposed leaves (17% of total weight) was further separated in morphotypes, identified (with the aid of the exsiccate collection made for this experiment) and weighed separately. Twenty-eight plant species, out of 48, were represented in the leaf litter (Table 1). Each sample was composed on average by seven different species (min. 4; max. 11), and the five more abundant species were: *Lithraea brasiliensis* Marchand ("aroeira-preta", ANACARDIACEAE), *Machaerium stipitatum* (DC.) Vogel ("sapuva", FABACEAE), *Myrsine umbellata* Mart. ("capororoca", MYRSINACEAE), *Roupala brasiliensis* Klotzsch ("carvalho-brasileiro", PROTEACEAE) and *Inga vera* Willd. ("ingá", FABACEAE) (Table 1). These five species occurred together in 10% of the samples. These five plant species represent food sources that are more likely to be encountered by the isopods when foraging, and therefore they were chosen for the feeding trials and further characterized in respect to chemical and mechanical properties.

Paleartic deciduous trees chosen for the study were common representatives of temperate forests inhabited by woodlice (Zimmer & Topp 2000; Zimmer 2002a): *Acer pseudoplatanus* L. ("sycamore maple", SAPINDACEAE), *Alnus glutinosa* L. ("alder", BETULACEAE), *Betula pendula* Roth ("birch", BETULACEAE), *Quercus robur* L. ("oak", FAGACEAE) and *Fagus sylvatica* L. ("beech", FAGACEAE). Henceforth plants will be referred by their generic names.

Plant leaf traits

For each neotropical species, a number of leaf traits were measured, which were grouped into structure-related, nutrient-related traits and secondary compounds to improve clarity. Structure-related traits were: a) leaf thickness, obtained with a digital caliper (n=15); b) leaf toughness, obtained with a penetrometer following the method of Graça & Zimmer (2005) (n=10); c) neutral detergent fiber (NDF = lignocellulose + hemicellulose), acid-detergent fiber (ADF = lignocellulose), lignin and cellulose, measured with method of Van Soest, Robertson & Lewis (1991). Nutrient-related traits were: a) organic matter, obtained after combustion at 500ºC; b) total nitrogen, obtained by Kjedahl method; c) total carbon, measured in a C/N Analyzer; d) calcium and phosphorous, obtained using the atomic absorption essay; e) total lipids, measured gravimetrically after extraction with sulfuric ether; f) non-structural carbohydrates, measured gravimetrically and g) calorific content, measured with a bomb calorimeter (Parr Instruments). Secondary compounds were related to the phenolic content and activity of the leaves. Total phenolics were determined as described in Bärlocher & Graça (2005), using commercially available tannin as standard (n=10) and phenolic activity was determined by the radial diffusion assay as described in Graça & Bärlocher (2005) (n=10). The radial diffusion assay quantifies the biological activity, i.e. the ability of phenolic compounds to bind and precipitate proteins (Graça & Bärlocher 2005).

With the exception of thickness, toughness and phenolics, traits were determined by the "Laboratório de Nutrição Animal – UFRGS", based on a sample of ≈500 g of leaf litter of each tree species.

For paleartic tree species, the following traits were obtained from the literature: toughness, lignin and cellulose (structure-related traits), N, P, Ca and C:N ratio (nutrient-related) and total phenolics.

Feeding assays

Feeding essays were conducted with adult, intermoult woodlice individuals, which were captured in the same day the essays started. Leaves from neotropical plants were collected from the ground in the site described above. Leaves from paleartic plants came from a laboratory stock and isopods collected at the surroundings of Kiel University, Kiel. Care was taken to select only leaves with an entire and intact lamina.

The essays with neotropical isopods *Balloniscus* and *Atlantoscia* were conducted in Porto Alegre, Brazil. Multiple-choice feeding arenas consisted of Petry dishes of 15 mm diameter, lined with a layer of plaster to provide moisture and a plastic opaque shelter. Each arena had four leaf discs (6 mm diameter) of each plant species and one isopod. Consumption was measured as the area (mm^2) of each food type eaten, which was counted under a stereomicroscope and with the aid of milimetric paper. The essays with paleartic woodlice *Porcellio* and *Philoscia* were conducted in Kiel, Germany. The feeding arenas consisted of small plastic boxes (6 mm diameter), lined with plaster and a small brick piece was added to provide shelter. In these essays consumption was accessed as the amount of food eaten (mg). For that purpose, leaves were cut into pieces and dried at 45°C for 48h. About 5 mg of each food type was offered to the isopods. At the end, the remaining food was dried again and weighed. There were 15 repetitions for each isopod species, and essays were stopped when ≈50% of the most consumed food had been eaten.

Performance of *Balloniscus* feeding on neotropical leaves was accessed through the consumption and egestion rates and assimilation efficiency of each food type, offered individually. The arenas were made of petry dishes lined with plaster, as described above. Each arena contained one individual *Balloniscus*, and about 35 mg of leaves, which were previously cut into pieces and dried at 45ºC for 48h. There were ten 10 repetitions for each food type. The experiment lasted for 96 hours. After that, the remaining food and the fecal pellets were dried and weighed. Isopod dry weight was estimated as 70% of fresh weight. Consumption and egestion rates 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 was the percentage assimilated from the amount consumed.

Data analysis

Relative consumptions of each food type in the multi-choice feeding experiments were compared trough two-way ANOVA, the factors being leaf species and isopod species. Proportion data was transformed (arc-sin of square-root) to ensure homoscedasticity (Underwood 1997).

To detect the general trends of leaf traits among plant species, we ran a principal component analysis (PCA) based on the correlation matrix of variables, on the complete dataset of traits of neotropical leaves (16 traits x 5 species) and on a smaller subset of traits of neotropical and paleartic leaves (8 traits x 10 species). These procedures originated two PCA sets of scores that were used for different purposes. The first one was used to relate trends in neotropical leaves to the preference and performance of *Balloniscus*. The second was used to relate trends in leaves to the preference of paleartic and neotropical isopods. To access the relationship between the observed food consumptions and leaf traits we follow the approach of Diaz et al. (2004). The response variables were correlated (Spearman correlation) to PCA scores obtained from the subsets as explained above. In this analysis we included only PCA axes that explained more than 20% of the variance.

Results

Leaf traits of neotropical plants

The leaves of neotropical plants evaluated in the present study differed notably in their chemical and mechanical properties (Table 2). With respect to energy content, all five species were isocaloric (Table 2). *Inga* differed from the others by exclusively showing a high density of trichomes in its abaxial face. The neotropical plants differed in respect to the total content of phenolics (ANOVA $F_{5,48}$=31.469; p<0.001) and phenolic activity (ANOVA $F_{5,49}$=20.046; p<0.001)(Fig. 1). *Roupala* and *Lithraea* showed the highest concentrations of phenolics (tannin equivalents), with a mean of 3.37% and 2.33% of the leaf dry weight, respectively, while the other three had about 0.7% only (Fig. 1). The activity of the phenolic compounds corresponded to the total phenolic content in the leaves, being much higher in *Roupala* and *Lithraea* than in the others (Fig. 1).

The first PCA axis, which explained 47.2% of the variance, was composed mainly of structure-related traits, being related to toughness, organic matter and thickness. Axis 2 was more related to nutrient-content of the leaves while Axis 3 was more related to secondary compounds (Table 3). In fig. 2 we can see the position of neotropical species along PCA axes 1 and 2 (78.1% of variance explained). Along axis 1 it separates *Roupala* from the others as having increased toughness, thickness, C:N ratio and phenolic activity. *Roupala* leaves were thicker and much tougher than the other species. It was also poor in nitrogen, calcium and phosphorous and presented the highest C:N ratio. The two leguminosae N-fixing trees, *Inga* and *Machaerium* showed the highest nitrogen content and, as expected, the lowest C:N ratios. *Machaerium* had the thinner and softer leaves (Table 2; Fig. 2). Along PCA axis 2

Myrcine is separated from the other as having increased amounts of lipids and carbohydrates (Fig. 2), and it was also richer in calcium (Table 2).

Comparison between neotropical and paleartic tree species

Data on eight traits of paleartic tree leaves, gathered from the literature, are showed in Table 4, and Table 5 shows the results of the PCA considering both neotropical and paleartic tree species. Both axes 1 and 2 were composed by structural- and nutrient-related traits, and the third to secondary compounds (Table 5). Together they explained 76% of total variance. In general, neotropical leaves were tougher, ticker and had more lignin and calcium than paleartic species (Table 2) and higher C:N ratios, as can be seen in Fig. 3 and Table 2. Paleartic species were richer in P and cellulose. Axis 2 separated species with higher N:P ratios (*Alnus*, *Machaerium*) from those with lower N:P and high quantities of cellulose (*Betula*, *Acer*)(Fig. 3). Considering nutrient-, structure- and secondary compounds related traits, *Alnus* and *Machaerium* are nutrient rich, and poor in structure-related traits and secondary compounds while *Roupala* is the opposite (Fig. 3, Table 2).

Feeding preferences and performance

The multiple-choice feeding trials showed no differences in the feeding preferences among isopod species but very conspicuous differences among plant species in all feeding trials (Fig. 4).

Among neotropical plants, *Machaerium* was the preferred food while *Roupala* and *Inga* were clearly avoided by the neotropical isopods (Two-way ANOVA; LEAF $F_{4,150}=76.628$, $p<0.001$; ISOPOD $F_{1,150}=0.008$, $p=0.93$)(Fig. 4). *Philoscia* and *Porcellio* also avoided *Roupala* and *Inga*, but their food preferences were more towards *Lithraea* litter (Two-way ANOVA; LEAF $F_{4,145}=26.579$, $p<0.001$; ISOPOD $F_{1,145}=0.680$, $p=0.413$) (Fig. 4). While *Atlantoscia* and *Balloniscus* showed a clear preference rank from *Roupala* (-) to

Machaerium (+), paleartic isopods showed less conspicuous differences among *Myrcine*, *Lithraea* and *Machaerium*.

Among paleartic plants, *Alnus* was the preferred food of temperate isopod species (Two-way ANOVA; LEAF $F_{4,140}=66.232$, $p<0.001$; ISOPOD $F_{1,140}=1.176$, $p=0.28$) and neotropical (Two-way ANOVA; LEAF $F_{4,50}=32.275$, $p<0.001$; ISOPOD $F_{1,50}=0.455$, $p=0.50$). *Alnus* constituted more than 60% of the total amount consumed in the experimental units (Fig. 4). *Quercus* litter was clearly avoided by *Balloniscus* and *Atlantoscia*.

In the performance trials (when offered no choice of food), *Balloniscus* fed from all neotropical plants, but showed higher consumption rates of *Myrcine* and *Lithraea*. Assimilation efficiencies were higher when feeding on *Roupala* and *Inga* (Fig. 5). As the high the assimilation efficiencies of the least consumed species, *Roupala* and *Inga* are in fact due to slow digestion that leads to smaller production of fecal pellets during the course of the trials (Zimmer 2002b), we choose to use the consumption rates as the best indicator of performance in the next analysis.

Relationship between preference, performance and leaf traits

PCA scores of plants along axis 1 were positively correlated to preference of *Balloniscus*, but not to performance. This indicates that toughness, thickness, C:N ratio and phenolic activity were negatively correlated to feeding preference while the best performance (high consumption rates, in this case) was obtained in plants with intermediary values of those traits (Fig. 6; left column). The ordination of plants along axis 2 did not explained *Balloniscus* preference but was correlated to performance, indicating that higher consumption rates were positively correlated to increasing contents of carbohydrates and lipids and negatively correlated to increasing contents of cellulose, carbon and fiber (Fig. 6; right column).

Feeding preferences of paleartic and neotropical woodlice

The feeding preferences of paleartic and neotropical woodlice were all negatively correlated to tree species position along axes 1 and 2. This means that feeding preference increases with the decrease in thickness, C:N ratio, cellulose and phosphorous and increase in nitrogen and calcium content (Fig. 7). Combining the results of these correlations to the actual attributes values presented in Tables 2 and 4, we propose a template for woodlice (Crinocheta) feeding preferences (Fig. 8). Rejection of food by terrestrial isopods occurs when litter has: (1) high density of trichomes; (2) a combination of toughness >50 g mm^{-2} and C:N ratio >25; or (3) a combination of N <2%, C:N >25 and cellulose >30%. The preferred food is the one with N >2%, Calcium >1%, thickness < 0.1 mm. Among plants that fulfilled these last characteristics, neotropical isopods prefer leaves with C:N ratio <20 and lignin <20% while paleartic isopods showed preferences towards increased phenolic content (>2%). Accordingly, food is accepted (eaten in intermediate amounts) when leaves present traits with intermediate values to the rejected and the preferred (Fig. 8).

Discussion

Detritivores, such as terrestrial isopods, are likely to influence decomposition and nutrient cycling rates directly, through consumption of litter (Bocock 1964, Lavelle 1997), and indirectly by stimulation of microbial community activity (Zimmer & Topp 1999) and by being predated by soil fauna (Moore et al. 2004). Their populations, however, are likely to be bottom-up regulated and constrained not only by litter biomass but also by litter chemistry. Therefore, their decisions towards specific leaf litter types for feeding may influence decomposition processes as well as their population dynamics.

Amongst the variety of mechanisms employed by plants to defend their photosynthetic and growth tissues from herbivores and abiotic factors, three types are more likely to be retained after senescence and influence litter chemistry: reduction of nutrients; investment in structural compounds (Taylor et al. 1989) to grant leaf hardening by increasing lignin, cellulose and leaf thickness; and investment in chemical defenses through the production of secondary compounds (Coley et al. 1985, Findlay et al. 1996, Schoonhoven et al. 2005). All these factors are known to influence, at least to some extent, palatability to herbivores (Pennings & Paul 1992, Wardle et al. 2002, Pérez-Harguindeguy et al. 2003), and, as pointed out by Pennings et al. (1998), attempts to predict their diet choices based only on one trait has limited success, nonetheless relatively few studies have compared the importance of multiple plant traits. In accordance to that observation, the first main conclusion of our study is that feeding preferences of woodlice are determined by a combination of multiple plant traits. The three types of defences cited above will influence different stages of the whole feeding and digestion process and it seems appropriate that isopod decision towards a specific food should be the one that maximizes both nutrient uptake and assimilation.

Structure-related traits are likely to regulate nutrient intake rates, firstly by making the processing of the plant material by the mouthparts more difficult and secondly by slowing down digestion. The presence of trichomes, for instance, may completely impede leaf ingestion. The breakdown of lignin and cellulose, although possible, requires a number of enzymes and energy, while they impede the access to nutrients inside leaf cells (Taylor et al. 1989, Zimmer 2002b). This digestive process of recalcitrant plant material by woodlice are mainly due to enzymes secreted by the hepatopancreatic symbionts and also due to microbiota ingested with food (Zimmer 2002b), and the oxidative processes of lignocellulose degradation are favored by some physiological gut characteristics (Zimmer & Brune 2005). Soma & Saitô (1983) demonstrated the influence of toughness in the choice among different decaying stages of *Pinus thunbergii* Parl. needles by *Porcellio scaber*. The rejected type had >30% in lignin content while the preferred had only 6.5% lignin and was also 85% softer than the rejected food. Catalán, Lardies & Bozinovic (2008) offered four types of sclerophyllous vegetation to *Porcellio laevis*. The offered food ranged from 13% to 23% in cellulose, 18% to 47% in lignin and 30% to 69% in ADF content, and all had C:N ratios >52. They verified preferences towards *Colliguaja odorifera* Molina which, compared to the other species, had the lowest values of these traits (Catalán et al. 2008). The influence of trichomes leading to the rejection of food irrespective of other favorable traits has been demonstrated only once, by Dudgeon, Ma & Lam (1990). Isopods rejected a litter with very hairy leaves, in spite of its high cooper content and low amounts of secondary compounds.

The presence of secondary compounds such as phenolics are likely to regulate nutrient assimilation, because they interact negatively with gut microbiota, which provides necessary digestive enzymes. Zimmer (1999) showed that feeding of an artificial diet rich in tannic acid reduces the counts of microorganisms in the gut of *P. scaber*, which therefore have to rely solely on the endosymbiotic bacteria of the hepatopancreas for the oxidation of phenolics. On the other hand, gallic acid in the diet (2%) reduced the number of palatable fungi and bacteria less strikingly, and increased the total number of the gut microbiota. Zimmer et al. (2002) showed that the presence of a variety of phenolic compounds, such as tannin, ferulic acids and quebracho, do not deter feeding by paleartic woodlice and, at least on *P. scaber*, the harmful effects of ingested phenolics are prevented by high concentrations of surfactants in the gut fluids (Zimmer 1997). The ability to oxidize phenolics increases from marine to semiterrestrial to terrestrial species (Zimmer *et al.* 2002) and therefore represents an important adaptation to the terrestrial lifestyle (Zimmer 2002b). There are intraspecific differences in the ability to digest phenols, and this may explain why paleartic species consumed more from *Lithraea* than the neotropical species. The negative effects of phenolic compounds may be enhanced when the litter is also though and fiber rich, as the decrease of gut microbiota would slow down its breakdown and retard nutrient release. This relationship explains why isopods were capable of feeding on *Lithraea*, which was very rich in phenolics with a high capacity of precipitating proteins, but were never seen feeding on a litter that was both very tough and rich in phenolics, as *Roupala* in our study. Other studies have also related feeding avoidance to the presence of secondary compounds. Dudgeon et al. (1990) verified that four sympatric woodlice species showed the same preference ranking, being *Berchemia racemosa* Siebold & Zucc and *Celtis sinensis* Pers. the most preferred and *Uvaria* *microcarpa* Champ. ex. Benth. and *Cinnamomun camphora* L. avoided by the isopods. The authors attributed the preferences to a low percentage of soluble tannins in both high *B. racemosa* (1.56%) and *C. sinensis* (0.79%) and to a high calcium content in *C. sinensis* (10.57% by weight). The avoidance of *C. camphora* was probably due to the presence of terpenes and the alkaloid reticuline (Dudgeon et al. 1990). Woodlice also preferred to feed from plants that contained alkaloids but these are very rapidly degraded rather than on plants that contained contain resistant polyphenols (Hassall & Rushton 1984).

Nutrient-related traits are obviously important to isopod nutrition and influence their fitness (Lardies et al. 2004). Several studies have showed that nutritional items in the diet (protein and carbohydrates) have important consequences on female life history and offspring growth of several woodlice species (Rushton & Hassall 1983, Lavy et al. 2001, Lardies, Carter & Bozinovic 2004). Our results with *Balloniscus* showed that while feeding preferences were driven by low thickness, thoughness and fiber contents and high amounts of N, P and Ca, consumption rates were driven by lipids, carbohydrates and Ca contents. From that we arrive at our second conclusion, which regards the differential influence of leaf traits on feeding preferences and performance. Several works have pointed out that consumption rates in single choice chambers to not always match feeding preferences on multi-choice experiments (Rushton & Hassall 1983, Dudgeon et al. 1990). Dudgeon et al. (1990), for instance, showed that while feeding preferences were towards *B. racemosa*, higher feeding rates were verified in *C. sinensis*, which had the highest Ca contents and lowest content of phenolics.

It is clear from the present and past studies that woodlice are able to discriminate among food types. The third conclusion that arrives from this study is that woodlice species, at least in the Crinocheta section, present a common mechanism of food recognition. Unfortunately, discussion on this topic is limited because to date almost nothing is known about the underlying mechanisms of food choice due to lack of knowledge on the chemoreceptory capabilities of terrestrial isopods (Zimmer 2002b). Chemoreceptors are thought to be located on the antennae (Hoese 1989), antennulae (Schmalfuss 1998) and mouthparts (Zimmer 2002b), constituting the site for contact chemoreception. Seellinger (1983) identified olfactory cells, that responded to fatty acids, aldehydes, amines and grass extracts, and four groups of gustatory cells in the desert species *Hemilepistus reaumuri* (Milne-Edwards, 1840): sugar cells; calcium cells; amino acid cells and cells that responded only to extracts of other desert woodlice. Latter, Zimmer, Kautz & Topp (1996) showed that *P. scaber* is capable of orientate towards air-borne metabolites.

Finally, we demonstrated that a similar suites of traits that governs decomposability of litter and vegetation responses to herbivory (Cornelissen et al. 1999; Wardle et al. 2002, Pérez-Harguindeguy et al. 2003), also determines palatability to detritivores. Litter-quality changes induced by herbivory or other environmental changes, thus, can affect food selection and overall litter consumption by macrofauna. This behavior has consequences for decomposition and nutrient mineralization (Hättenschwiler & Bretscher 2001). Wardle et al. (2002) indicated that good quality litter tend to promote decomposition of other litters and poor litter tend to decompose more rapidly when mixed with other litter types. These results clearly show that macrofauna presence can be an important driver of litter-species diversity effects, when inhabiting an environment of diverse leaf litter layer and feeding selectively on them (Hättenschwiler & Gasser 2005). Kautz & Topp (2000) highlighted that *Alder glutinosa* is used as a shelter or nursery plants in plantations of monocultures such as *Quercus robur*, as they have a positive effect in their co-occurring plants through N-fixation. Since its litter is consumed at higher rates, large amounts of feces are incorporates to the topsoil and are significant to plant nutrition especially in conditions of low soil fertility. Based on our results, the presence of *Machaerium stipitatum* and its consumption by woodlice may have the same effect on neotropical forests, benefiting slow decomposing litter such as *Inga* and *Roupala*.

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Table 1. List of dicotyledonous tree species found in a 1-ha fragment of neotropical forest in southern Brazil whit their frequency of occurrence and total weight in the leaf litter (based on 40 leaf-litter samples). Empty cells indicate that the respective species was not found in the litter samples. In bold, species addressed in this study.

Family	Species	Frequency (%)	Total weight (g)
ACANTHACEAE	*Justicia brasiliana*	-	-
ANACARDIACEAE	***Lithraea brasiliensis***	80.0	42.90
	Schinus molle	2.5	0.24
ANNONACEAE	*Rollinia sylvatica*	-	-
ARECACEAE	*Syagrus romanzoffiana*	-	-
ASTERACEAE	*Gochnatia polymorpha*	-	-
CANELLACEAE	*Citronella paniculata*	-	-
CLUSIACEAE	*Garcinia gardneriana*	7.5	2.40
EBENACEAE	*Diospyros inconstans*	22.5	2.30
ERYTHOXYLACEAE	*Erythroxylum argentinum*	2.5	0.06
EUPHORBIACEAE	*Gymnanthes concolor*	15.0	1.21
	Sebastiania brasiliensis	-	-
	Sebastiania serrata	7.5	1.20
FABACEAE	***Inga vera***	40.0	39.24
	Machaerium stipitatum	67.0	13.01
LAMIACEAE	*Vitex megapotamica*	-	-
LAURACEAE	*Nectandra megapotamica*	2.5	0.11
	Nectandra oppositifolia	-	-
	Ocotea catarinensis	30.0	9.45
MALVACEAE	*Luehea divaricata*	10.0	2.57
MELIACEAE	*Trichilia claussenii*	2.5	0.09
	Trichilia elegans	2.5	0.03
MONIMEACEAE	*Hennecartia omphalandra*	-	-
MORACEAE	*Sorocea bonplandii*	25.0	1.31
MYRSINACEAE	*Myrsine coriacea*	20.0	17.52
	Myrsine umbellata	87.5	127.04

MYRTACEAE	*Campomanesia xanthocarpa*	27.5	4.30
	Eugenia schuechiana	2.5	0.29
	Myrcianthes pungens	-	-
	Myrciaria cuspidata	2.5	0.03
NYCTAGINACEAE	*Guapira opposita*	-	-
PROTEACEAE	***Roupala brasiliensis***	45.0	41.37
ROSACEAE	*Prunus myrtifolia*	-	-
RUBIACEAE	*Faramea marginata*	-	-
	Psychotria leiocarpa	-	-
RUTACEAE	*Zanthoxylum rhoifolium*	-	-
SALICACEAE	*Banara parviflora*	15.0	3.85
	Casearia decandra	-	-
	Casearia sylvestris	-	-
	Xilosma pseudosalzmanii	25.0	12.24
SAPINDACEAE	*Allophylus edulis*	37.5	5.67
	Cupania vernalis	75.0	28.32
	Matayba elaeagnoides	15.0	3.49
SAPOTACEAE	*Chrysophyllum marginatum*	-	-
SOLANACEAE	*Cestrum strigilatum*	-	-
STYRACACEAE	*Styrax leprosus*	-	-
URTICACEAE	*Cecropia pachystachya*	5.0	1.55
	Coussapoa microcarpa	20.0	3.42

Table 2. Structure-related and nutrient-related leaf traits of neotropical woody semi-deciduous and evergreen species.

	Roupala brasiliensis	*Myrsine umbellata*	*Lithraea brasiliensis*	*Inga vera*	*Machaerium stipitatum*
Structure-related traits					
Thickness (mm)	0.30	0.20	0.08	0.12	0.03
Toughness (g mm^{-2})	105.67	47.26	39.14	37.96	29.57
Trichomes	absent	absent	absent	present	absent
NDF (%)	71.52	54.46	59.93	75.86	57.78
ADF (%)	59.59	46.25	48.60	62.14	41.63
Lignin (%)	39.45	33.75	34.28	45.14	20.86
Cellulose (%)	20.14	12.5	14.32	17.00	20.77
Ash (%)	4.31	6.03	7.51	5.17	8.60
Nutrient-related traits					
Nitrogen (%)	1.10	0.90	2.30	2.84	3.72
Carbon (%)	69.90	30.40	70.09	59.91	69.19
C:N ratio	63.69	33.81	30.42	21.12	18.58
Calcium (%)	0.61	1.50	1.20	0.78	1.40
Phosphorous (%)	0.04	0.03	0.18	0.06	0.14
Lipids (%)	3.50	7.04	4.22	1.95	3.49
Carbohydrates (%)	51.68	56.56	48.14	39.38	31.43
Energy (kcal kg^{-1})	4943.84	4925.8	4891.3	4767.03	4852.7

Table 3. Scores of plant traits in three main PCA axes, obtained from a matrix of 16 traits x 5 plant species (Neotropical). The five highest scores for each PCA axis are indicated in bold.

Traits	**PCA 1 (47.2%)**	**PCA 2 (30.9%)**	**PCA 3 (14.5%)**
Structure-related			
Toughness	**-0.317**	0.039	0.214
Thickness	**-0.314**	0.165	0.010
Cellulose	-0.054	**-0.333**	0.202
Lignin	-0.263	-0.018	**-0.317**
ADF	-0.290	-0.153	-0.241
NDF	-0.243	-0.273	-0.210
Nutrient-related			
C:N ratio	**-0.302**	0.105	0.268
Organic matter	**-0.328**	0.038	-0.226
Carbohydrates	-0.186	**0.360**	0.036
Carbon	-0.035	**-0.346**	**0.361**
Lipids	0.067	**0.421**	0.058
Phosphorous	0.217	-0.137	**0.347**
Nitrogen	0.228	**-0.331**	-0.018
Calcium	0.298	0.225	0.034
Secondary compounds			
Phenolic activity	**-0.306**	-0.011	**0.303**
Total phenolics	-0.224	0.013	**0.464**

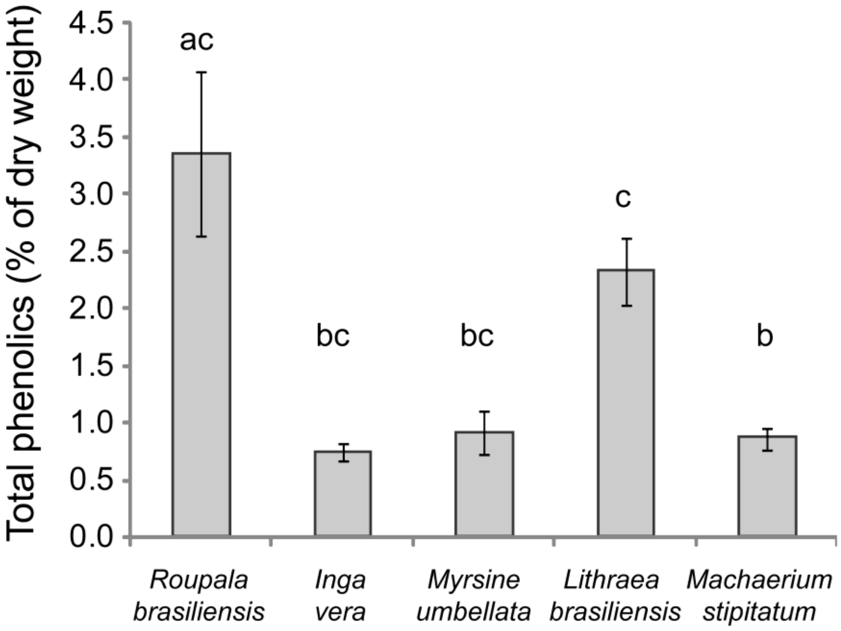
Table 4. Structure-related and nutrient-related leaf traits and secondary compounds of Paleartic woody deciduous species. References. A) present study; B) Pâhlsson 1989; C) Gessner 1991; D) Barlocher, Canhoto & Graça 1995; E) Cotrufo, Ineson & Roberts 1995; F) Cortez et al. 1996; G) Zimmer & Topp 1997; H) Cotrufo, Briones & Ineson 1998; I) Zimmer 1999; J) Weber-Blaschke, Claus & Rehfuess 2002; K) Brozec & Wanic 2002; L) Zimmer & Topp 2000; M) Hoorens, Aerts & Stroetenga 2003; N) Kazda et al. 2004; O) Gessner 2005; P) Portsmuth & Niinemets 2006; Q) Giertych et al. 2006; R) Hobbie et al. 2006; S) Kalbitz, Bargholz & Dardenne 2006; T) Vauramo et al. 2006; U) Hedde et al. 2007; V) Silvfer et al. 2007; W) Lecerf & Chauvet 2008; X) Weber-Blaschke et al. 2008.

	Acer pseudoplatanus	*Alnus glutinosa*	*Betula pendula*	*Quercus robur*	*Fagus sylvatica*
Structure-related traits					
Thickness (mm)	0.08[A]	0.09[A]	0.09[A]	0.11[A]	0.08[A]
Toughness (g mm^{-2})	17-30[G]	12-13[L]	19-22[L]	41-58[L]	N/A
Lignin (%)	9.1[H] 16.6[R] 11.00[S]	8.00[C] ≈19.00[I] 13.00[W]	≈15.00[I] 40.8[R] 9.21-16.04[V]	≈30.00[I] 23.3[R]	31.5[F] 25.50[O] 24.5[R] 20.2[S]
Cellulose (%)	18.47[R] 16.60[S]	13.80[C] ≈44.00[I] 7.4[W]	≈45.00[I] 18.6[R]	≈50.00[I] 22.2[R]	32.20[O] 32.4[F] 23.1[R] 18.90[S]
Nutrient-related traits					
Nitrogen (%)	1.0 – 1.3[G] 0.5[H] 1.1 – 2.5[N] 2.0-3.0[X]	3.5[K] 3.2-3.5[L] 2.52[M] 2.8[Q] 2.1[W]	1.7-1.9[L] ≈1.6[P] 2.6[Q] 1.5 – 2.6[V]	1.6[L] 1.8[U]	0.7[F] 1.9[K] 1.8-2.7[N] 0.73[X]
C:N ratio	29.6[S]	14[K]	27-29[L]	28-30[L]	24.0[K]

		15-16[L]	≈20[T]	22.60[U]	36.1[S]
Calcium (%)	0.42 – 0.72[N] 2.1[R] 1.52[X]	1.80[K]	0.61 – 1.00[E] 1.15[R]	1.2[R]	0.50-1.0[B] 1.15[K] 0.32-0.52[N] 1.29[R]
Phosphorous (%)	0.51[J] 0.11[R] 0.15 – 0.20[X]	0.07[M] 0.03[W]	0.39-0.83[E] ≈0.35[P] 0.16[R]	0.05[M] 0.17[R]	0.11-0.15[B] 0.14[R]
Secondary compounds					
Total phenolics (%)	0.34 – 0.66[G]	0.66[D] 1.6-2.7[L] 0.91-1.76[W]	1.1 – 3.0[L]	1.5- 3.6[L]	5.0-8.0[B] 5.7[M]

Table 5. Scores of plant traits in three main PCA axes, obtained from a matrix of 8 traits x 10 plant species (five Neotropical and five Paleartic). The three highest scores for each PCA axis are indicated in bold.

Traits	**PCA 1 (38.5%)**	**PCA 2 (24.4%)**	**PCA 3 (13.1%)**
Structure-related			
Thickness	**0.52**	-0.02	0.08
Lignin	0.38	-0.27	**0.41**
Cellulose	-0.08	**0.46**	**0.27**
Nutrient-related			
Nitrogen	**-0.40**	-0.33	0.14
C:N ratio	**0.52**	0.13	-0.12
Phosphorous	-0.28	**0.55**	-0.14
Calcium	-0.24	**-0.50**	0.10
Secondary compounds			
Total phenolics	0.09	-0.21	**-0.83**



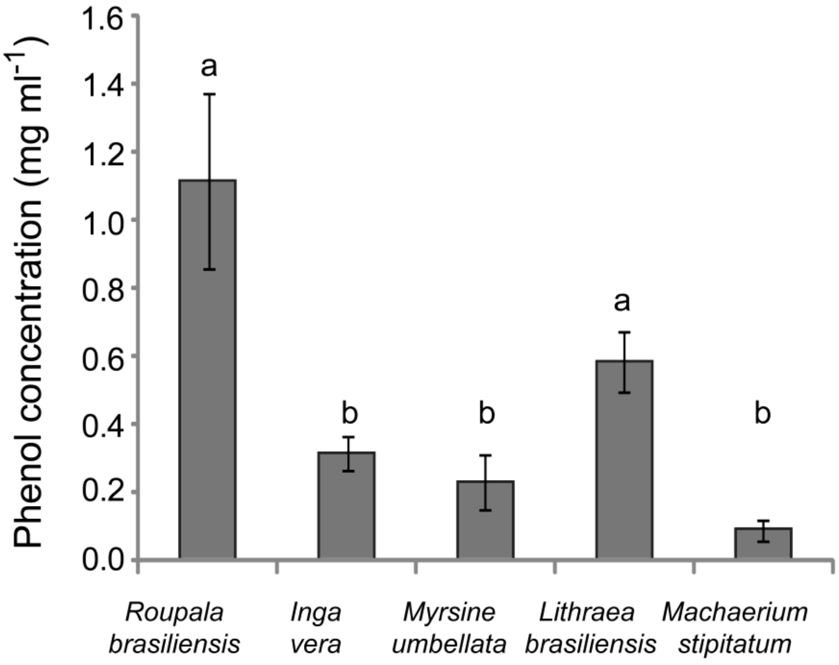


Figure 1. Total leaf phenolic content (top) and phenolic activity (bottom) of neotropical trees. Different letters indicate significant differences among diets (Tukey's *post hoc* test; $p<0.05$).

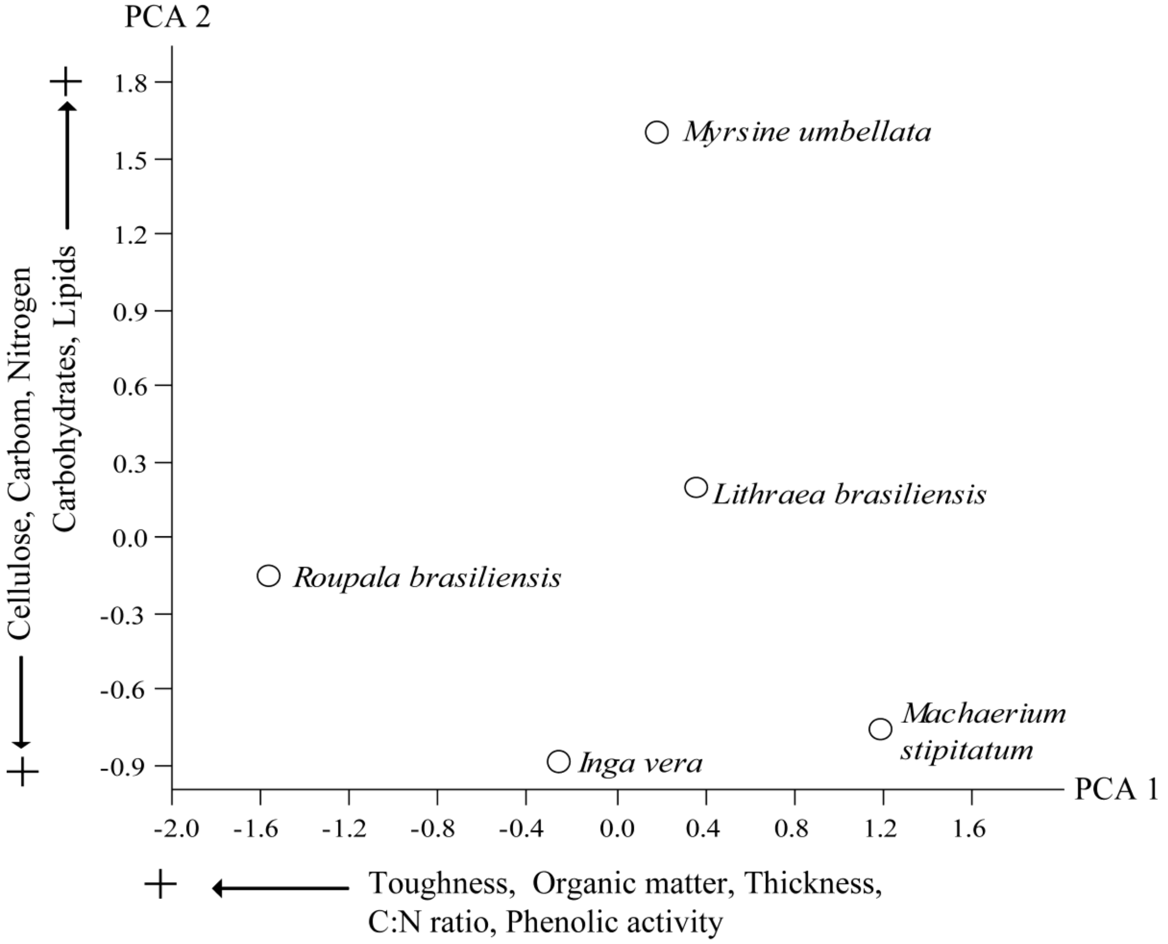


Figure 2. Principal component analysis of five Neotropical plant species on the basis of 16 traits. Data for PCA scores is shown in Table 3.

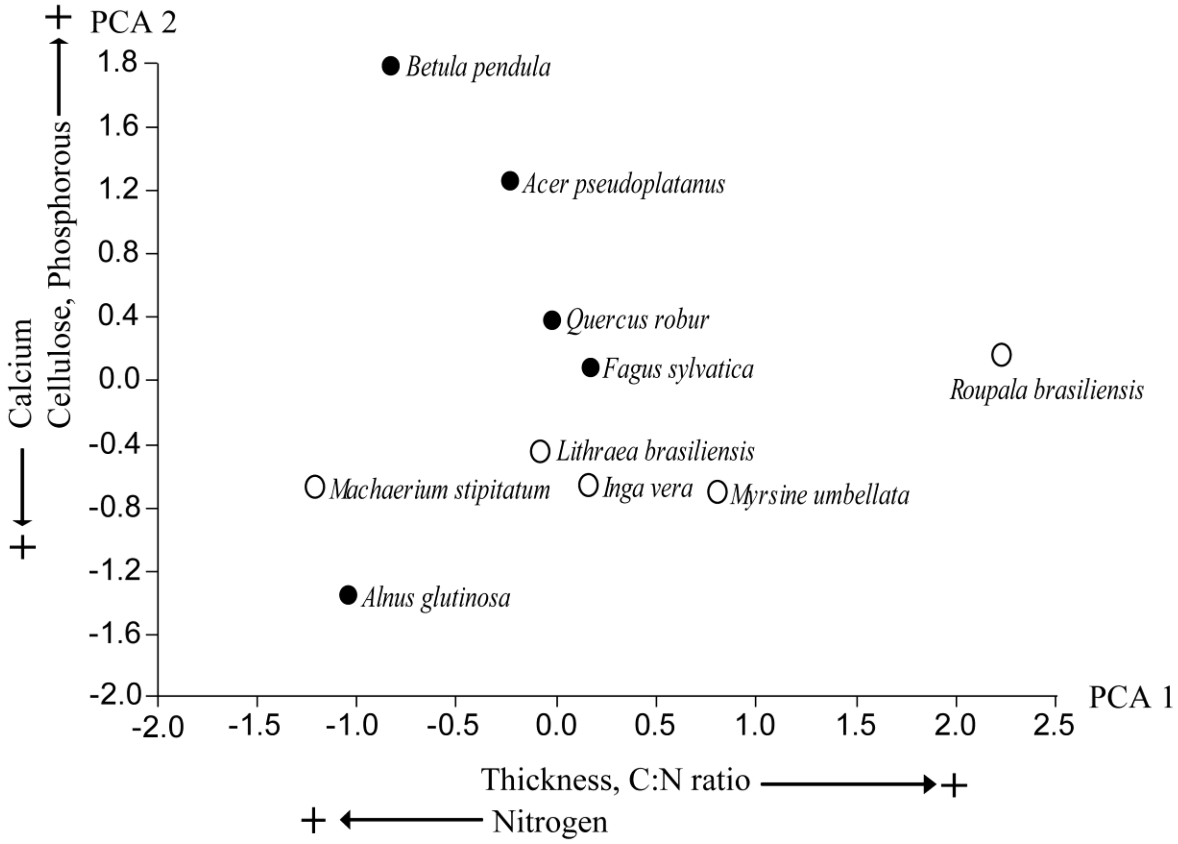


Figure 3. Principal component analysis of 10 plant species on the basis of 8 traits. Data for PCA scores is shown in Table 5.

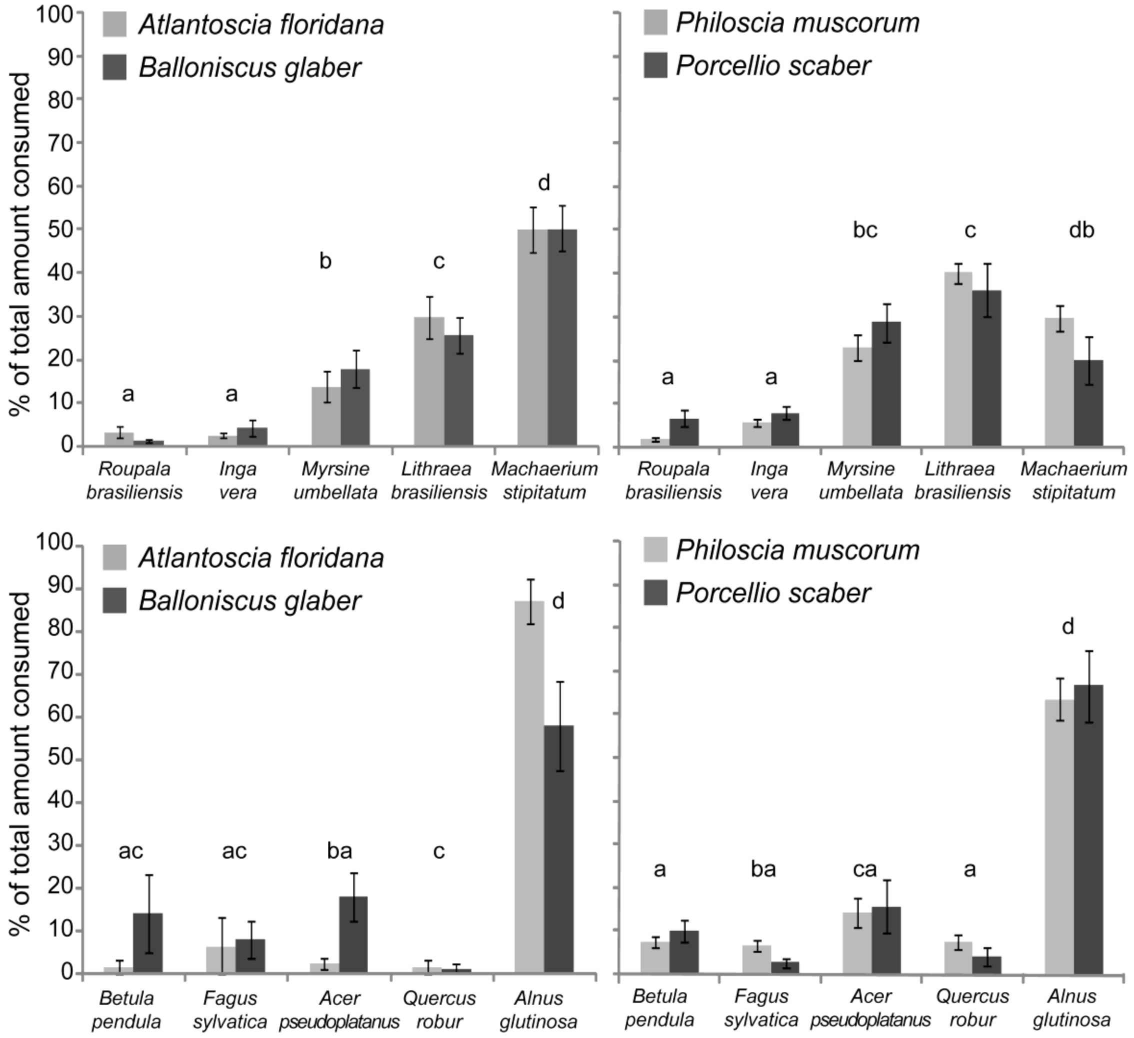


Figure 4. Feeding preferences of terrestrial isopods. In the left column are the neotropical isopod species, feeding on leaves of neotropical plants (top) and paleartic plants (bottom) and in the right column are the temperate isopod species. Values indicate the consumption of each diet from the total amount consumed in the multiple-choice feeding trials (mean ± S.E. in %). Different letters indicate significant differences among diets (Tukey's *post hoc* test; $p<0.05$).

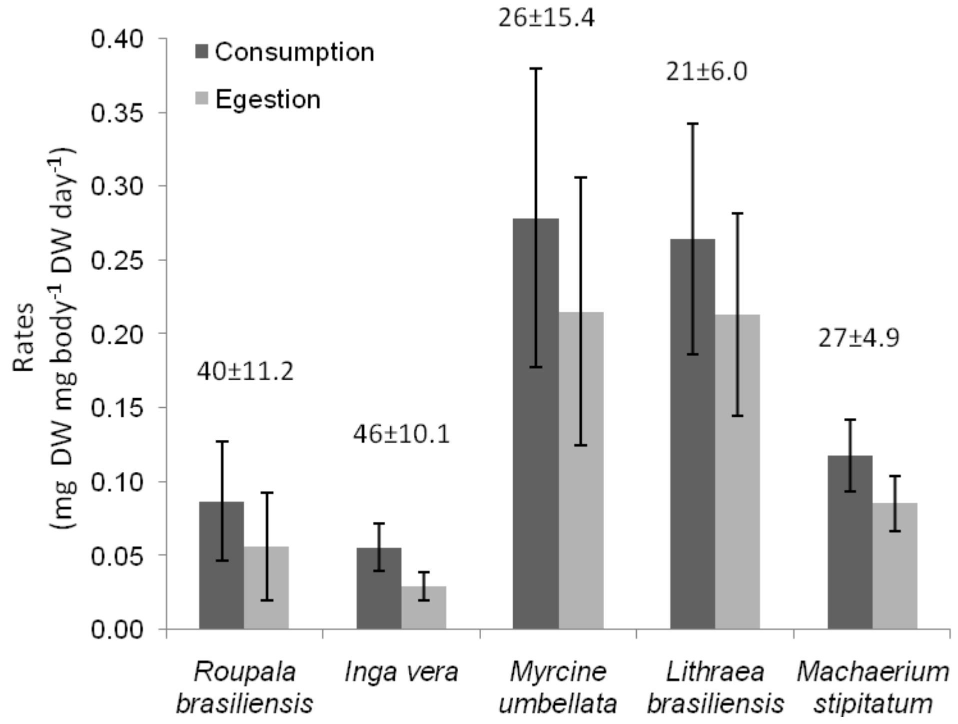


Figure 5. Mean (± 95% C.I.) consumption and egestion rates of *Balloniscus glaber* when feeding on leaf-litter of different Neotropical plant species. Values above bars indicate assimilation efficiency (mean ± 95% C.I.) on each diet.

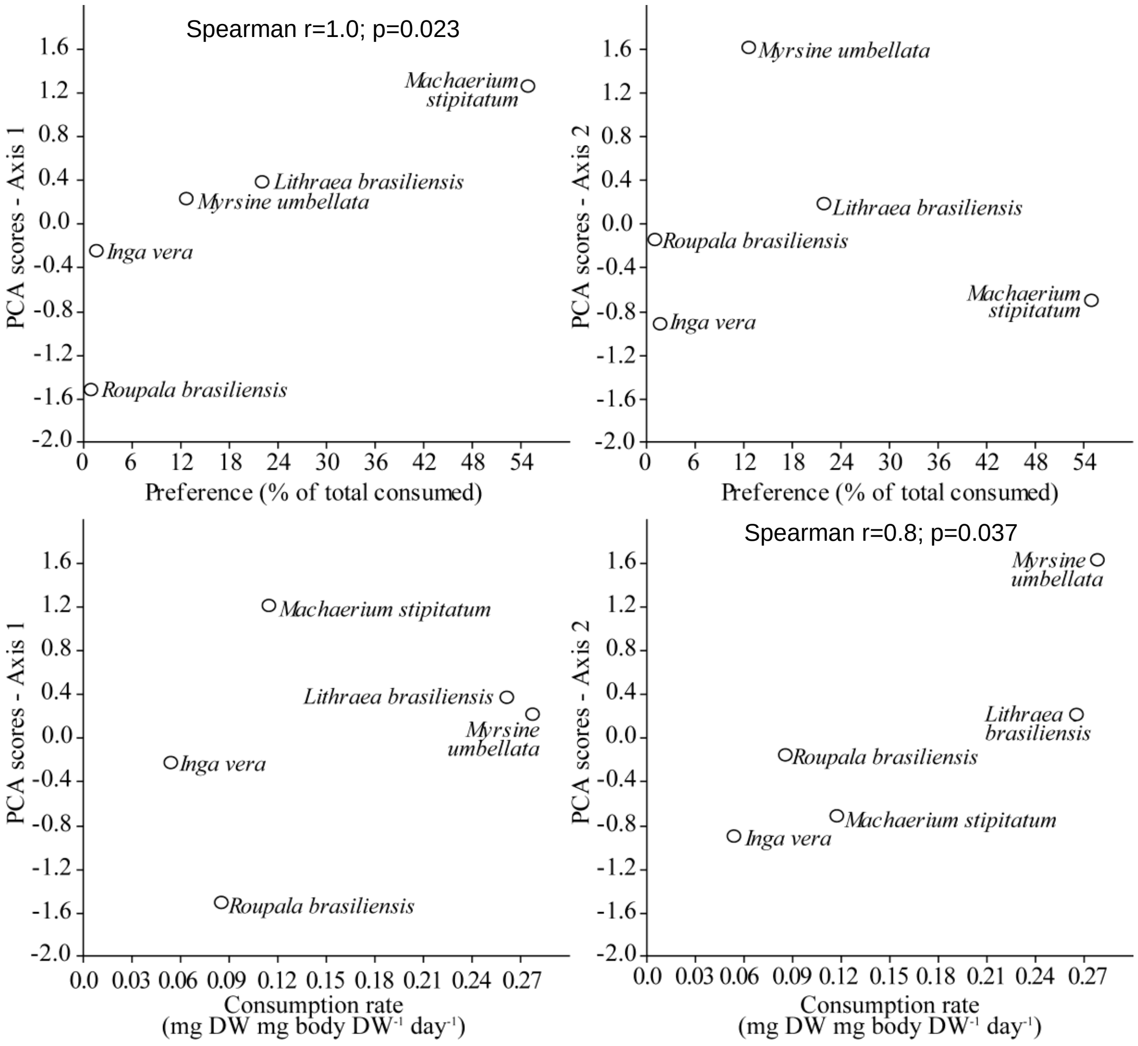


Figure 6. Relationships between leaf traits of neotropical trees, represented by their PCA scores and the preference, measured by the % consumed of each species (top figures), and performance, measured by average consumption rates of each tree species (bottom figures). All response variables refer to the isopod *Balloniscus glaber*. Refer to Table 3 for explanation of PCA axes.

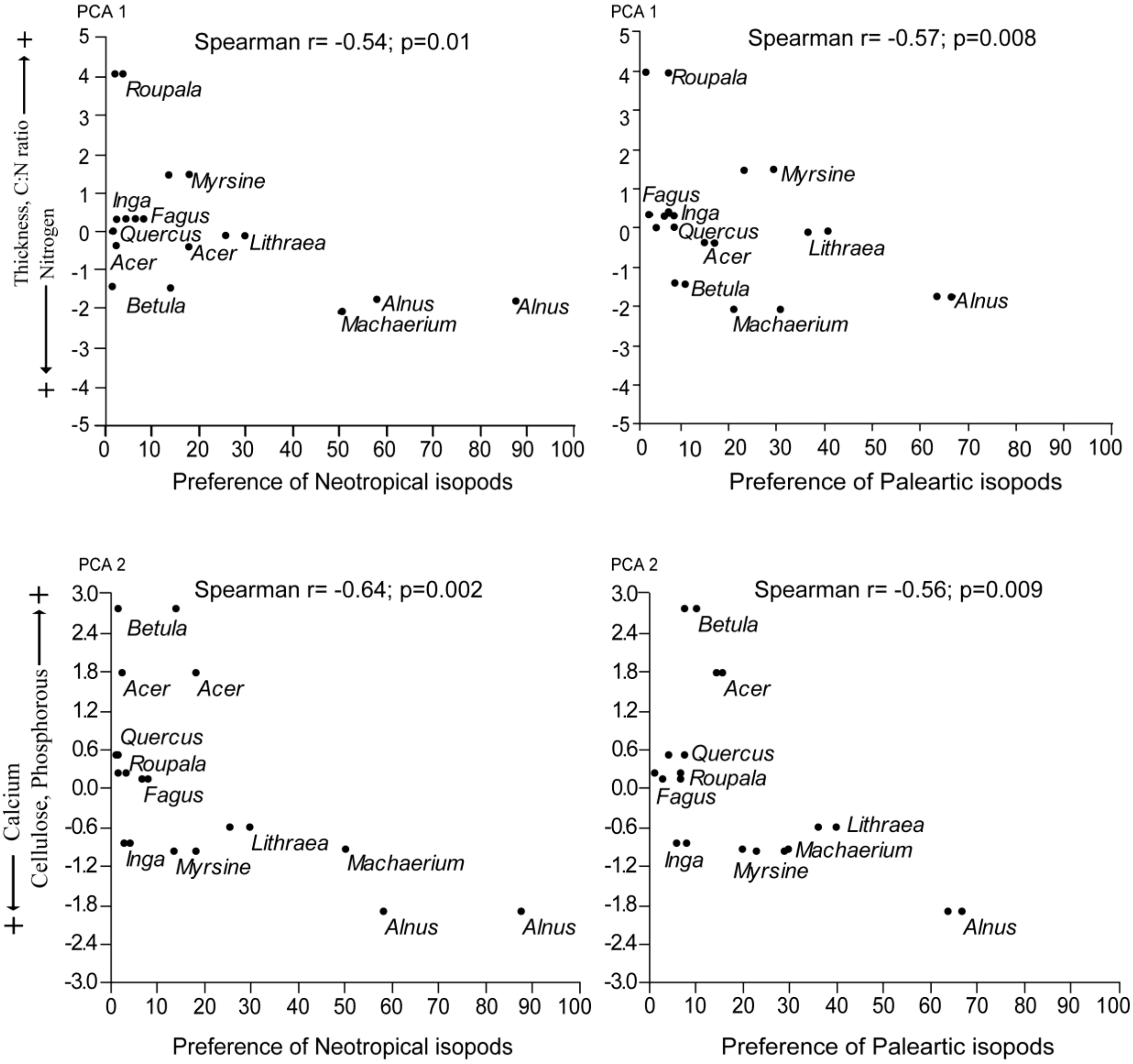


Figure 7. Relationships between leaf traits of neotropical and paleartic trees, represented by their PCA scores, and the preference, measured by the mean % consumed of each species by neotropical (right column) and paleartic isopods (left column). Figures on the top refer to axis 1, and on the bottom, to axis 2. Refer to Table 5 for explanation of these PCA axes. Spearman rank correlation values are given in the top of each figure.

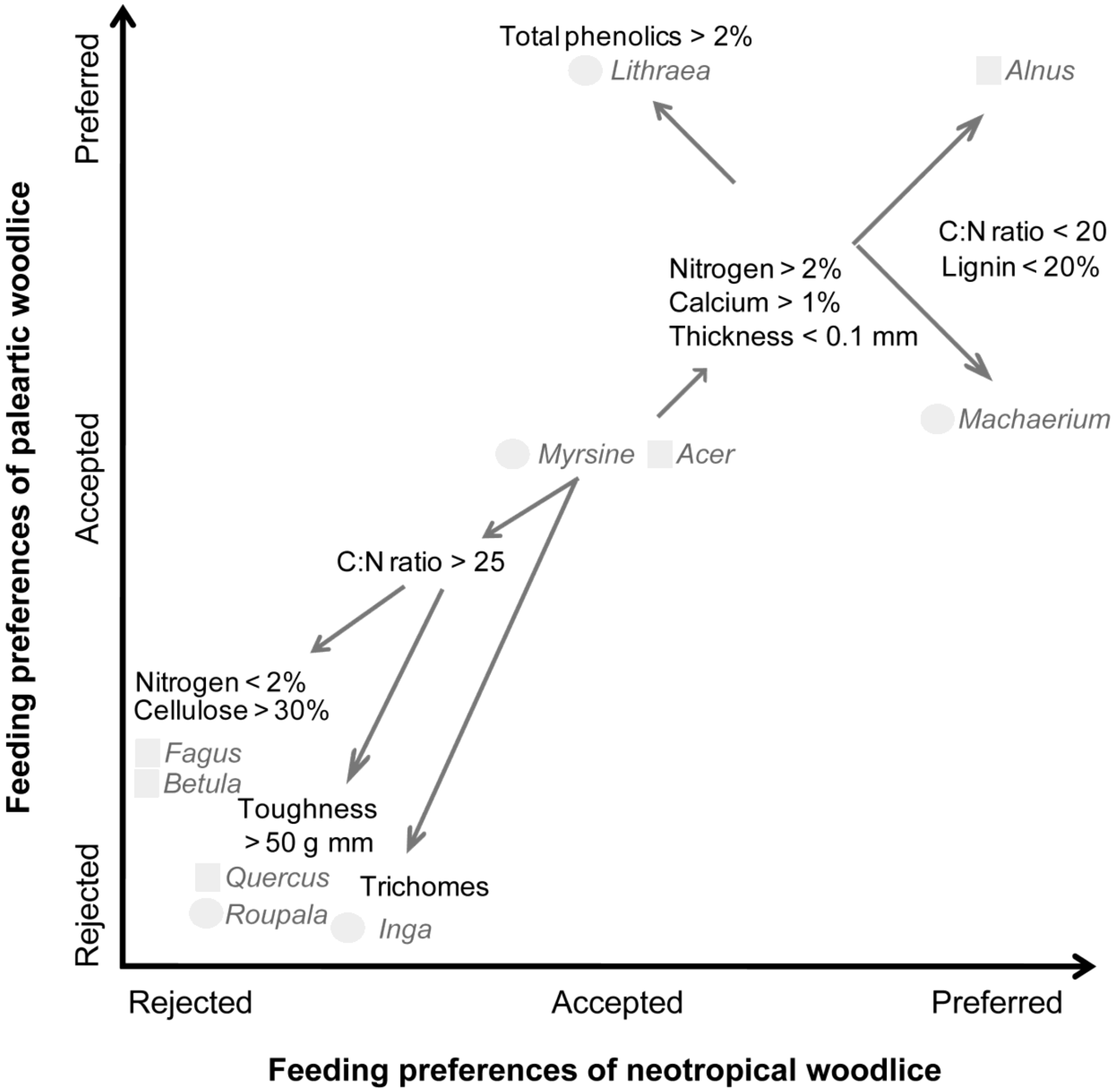


Figure 8. Template for the organization of the feeding preferences of terrestrial isopods (Crinocheta). Grey circles indicate neotropical tree species and squares indicate paleartic tree species.

Considerações finais

Do trabalho de campo realizado em 2004 e 2005 resultaram os capítulos I e II e muitas perguntas sobre a ecologia de *A. floridana* e *B. glaber*. Os capítulos III, IV e V que vieram a seguir tiveram como objetivos responder a algumas destas questões, e estes por sua vez originaram outras tantas dúvidas sobre a biologia e ecologia das duas espécies.

As primeiras questões foram relativas às diferenças entre a ecologia populacional. Para a captura das espécies foi ajustado o método de coleta, passando-se a coletar a camada mais superficial de solo além da serapilheira. Utilizando o método mais adequado, percebeu-se então que a densidade local de *B. glaber* era tão alta quanto à de *A. floridana*. Por ser uma espécie muito comum, muitas vezes encontrada em ambientes com pouca diversidade estrutural, era esperado que *A. floridana* fosse mais tolerante a variações climáticas relativas à temperatura e umidade. Entretanto, *B. glaber* melhor suportou a intensa seca do verão de 2005, visto que sua população se manteve estável em relação à densidade e não foi observada mortalidade das mancas, ao contrário de *A. floridana* (capítulo II). Concluiu-se que *A. floridana* seria mais suscetível à dessecação, apoiando-se nas informações populacionais e também na sua morfologia, pois o menor tamanho corporal e pulmões pleopodais menos desenvolvidos resultam em maiores perdas de água pelo tegumento. Sendo mais suscetível a dessecação, como suas populações se mantêm tão abundantes e como esta espécie é capaz de ocupar diversas paisagens, algumas até inóspitas? Procurou-se então algumas respostas nas suas estratégias reprodutivas. *Atlantoscia floridana* possui todas as características favoráveis à manutenção de altas densidades e uma boa capacidade de colonização de novas manchas. Seu crescimento rápido e alto investimento reprodutivo contrapõem a alta mortalidade, e suas estratégias reprodutivas assemelham-se àquelas encontradas em espécies invasoras (Capítulo III). Já *B. glaber* situa-se no outro extremo do contínuo r-K. As taxas de crescimento e consumo de alimento mais baixas (Capítulo I) e o longo tempo de gestação (Capítulo III) indicam que esta espécie possui um metabolismo mais lento, e esta característica ajuda a explicar o padrão reprodutivo observado, restrito aos períodos mais quentes do ano. Como nos oniscídeos a duração período intramarsupial é inversamente relacionada à temperatura, a reprodução durante o inverno acarretaria em um custo energético muito elevado para a fêmea, devido à nutrição dos filhotes e restrições à locomoção. Assim, em uma escala local, sua maior resistência à dessecação e maior sobrevivência (também relacionada ao hábito escavador) garantem a estabilidade das densidades populacionais, mas *B. glaber* não tem a mesma capacidade para crescimento em número como *A. floridana*. Como ressaltado no Capítulo III, estas características expõem *B. glaber* a um maior risco de extinção.

Devido à distribuição agregada, é comum a obtenção de amostras com mais de 100 indivíduos e outras, muito próximas, sem nenhum. À medida que os trabalhos de campo mensais eram realizados, percebeu-se que indivíduos de *Atlantoscia* e *Balloniscus* ocorriam em altas densidades nas mesmas amostras, caracterizando assim populações sintópicas, além de simpátricas. Esta alta similaridade na distribuição espacial em pequena escala, sugeriu que as espécies apresentavam as mesmas preferências para ocupação de hábitat, provavelmente devido à semelhanças nas suas necessidades de umidade, temperatura, alimento e abrigo. Destas observações surgiram as perguntas sobre partição de hábitat e alimento. Seriam as espécies competidoras? Ocorreria competição por interferência ou exploração ou entre elas? Estas foram as questões que levaram à observação do comportamento das espécies em condições de laboratório (Capítulo IV). Comparando-se as atividades das espécies, quando juntas e separadas, foi possível constatar que há na verdade um alto grau de tolerância entre elas, com ausência de atos de agressividade. Foi confirmado o hábito escavador de *B. glaber* e foram demonstradas as diferenças no uso de abrigos durante o descanso, as quais possivelmente atuam como facilitadoras da coexistência. Entretanto, em relação ao alimento, ficou evidente a sobreposição do uso de recursos (Capítulo V), em condições de alimento limitado, talvez possa ocorrer competição por exploração entre as espécies.

A estimativa da participação dos isópodos no processamento da serapilheira, apresentada no Capítulo I, constituiu o primeiro passo em direção ao conhecimento do papel destes organismos nos solos de florestas neotropicais. Foi evidenciado que a biomassa das populações têm uma grande influência na participação de cada espécie na ciclagem de nutrientes. Além disso, os resultados dos experimentos sobre preferência alimentar indicam que os isópodos contribuem para o aumento das taxas de decomposição, alimentando-se preferencialmente de folhas de decomposição mais rápida, as quais contribuem para a decomposição do material vegetal mais recalcitrante.

Como perspectivas futuras, há ainda muitas questões interessantes sobre a ecologia destas espécies. A generalidade do modelo para as preferências alimentares deve ser testado frente à outras espécies de isópodos e outras combinações de plantas. Outras questões, especialmente em relação às particularidades de *B. glaber* são: Qual a influência da temperatura no tempo de desenvolvimento intramarsupial? Como é a dinâmica da reprodução em áreas mais frias? Em relação ao comportamento escavatório: Qual o papel da defesa dos buracos observados em laboratório (observação pessoal)? Qual o papel da agressividade entre os indivíduos (observação pessoal)? Será relacionado à reprodução ou defesa de recursos importantes? Existe competição pelos buracos (ou tocas)? As fêmeas passam mais tempo enterradas quando estão ovígeras? O hábito escavador garante uma maior sobrevivência às fêmeas ovígeras e aos indivíduos mais jovens (mancas)? Habitando solos úmidos e ricos em microorganismos, *Balloniscus* possui algum mecanismo para evitar a hipercarbia e a hipóxia? A estratégia de tanatose é realmente efetiva? Contra quais predadores? Por apresentarem tamanho corporal e estratégias anti-predatórias distintas, *Atlantoscia* e *Balloniscus* são predados por organismos diferentes? Qual a efetividade das duas estratégias?

É importante ressaltar que os resultados apresentados aqui diferem em muitos aspectos da ecologia conhecida dos isópodos terrestres a partir de estudos realizados na Europa. Existe um grande conhecimento acumulado sobre o grupo, mas este restringe-se à algumas poucas espécies ruderais, como *Armadillidium vulgare*, *Ligia* spp. e *Porcellio* spp., as quais têm sido utilizadas como modelo. Os resultados apresentados aqui ressaltam a importância do estudo de outras formas de vida e de diferentes biomas para um melhor entendimento da ecologia de isópodos terrestres. A fauna de isópodos neotropicais é muito rica em espécies, as quais apresentam diversas formas corporais e hábitos. Muitos padrões ecológicos e diferentes combinações de estratégias reprodutivas e comportamentais restam para serem descobertos e investigados.

Anexos

Nas páginas a seguir encontram-se as normas para publicação dos periódicos escolhidos para a publicação dos artigos desta tese, na seguinte ordem: *Revista Brasileira de Zoologia*, *Current Zoology* (anteriormente chamada *Acta Zoologica Sinica*), *Acta Oecologica*, *Journal of Insect Behavior* e *Functional Ecology*.

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Poinar, G. O., Jr., and Thomas, G. M. (1984). Laboratory Guide to Insect Pathogens and Parasites, Plenum Press, New York.

Contribution to a Book
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Functional Ecology

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Travis, J. (1994) Evaluating the adaptive role of morphological plasticity. *Ecological Morphology* (eds P.C. Wainwright & S.M. Reilly), pp. 99-122. University of Chicago Press, Chicago.
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