Oniscidea diversity across three environments in an altitudinal gradient in northeastern Rio Grande do Sul, Brazil

Elis Regina de Carvalho Lopes a, Milton de Souza Mendonça Jr. b, Georgina Bond-Buckup b, Paula Beatriz Araujo b,*

a Programa de Pós-Graduação em Oceanografia Biológica, Departamento de Oceanografia, Fundação Universidade Federal do Rio Grande, Av. Itália, Km 8, Caixa Postal 474, 96201-900 Rio Grande, RS, Brazil
b Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, pr. 43435, 91501-970 Porto Alegre, RS, Brazil

Available online 17 November 2005

Abstract

The diversity of Oniscidea across a 1000-m altitudinal gradient comprising three distinct environments—the coastal plain, the highland slopes, and the highlands—was described and analysed. We employed 1 h-long exploratory manual sampling at 41 sites. Fourteen species were identified, of 818 individuals collected. Sampling-effort curves stabilised for all three environments; analytical estimates of species richness did not exceed the observed value. Abundance did not vary significantly among environments, and local species richness differed only marginally. However, the Shannon diversity index for local sites indicated highland slopes to be significantly more diverse than the coastal region; the same was true for bootstrap estimates at the regional level. Two species appeared in all three environments, comprising 72.7% of the abundance. The coastal region and highlands had one exclusive species each, and the highland slopes had three. The first two environments are more similar to each other than to the slopes, although they are not contiguous. The altitudinal gradient of diversity was hump-shaped, because the highland slopes were most diverse. The reasons for this pattern are not biogeographical; that is, the highland slopes are not a contact zone between the highlands and the coast. A complete explanation depends upon better understanding of the effect of soil type and terrain slope on the diversity of terrestrial isopods.

© 2005 Elsevier SAS. All rights reserved.

Keywords: Crustacea; Terrestrial isopods; Diversity; Rio Grande do Sul; Brazil

1. Introduction

The majority of animals in terrestrial habitats are invertebrate members of the decomposer community, but soil is still one of the most poorly researched habitats of our planet [30]. Terrestrial isopods are fundamental representatives of the soil fauna, having an important role in terrestrial ecosystems [23]. Thus, knowledge of the isopod faunal richness of a region is one of the factors responsible for success in monitoring and conserving species. Work on the diversity of terrestrial isopods usually proceeds from a biogeographical perspective, focusing on distributions of species and species richness across regions or environments [12,20,21]. In other si-
tations, isopods are not the core group, and other taxa are included, as in [25], in which the diversity of five groups of soil arthropods, including Isopoda, was studied. No studies in Brazil have focusing on an analysis of oniscidean diversity. The northeastern portion of the State of Rio Grande do Sul, in southern Brazil, offers a variety of environments across short distances, because of the steep transition from the coast to the highlands (1000 m a.s.l.). Among the vegetation types are the restinga forests developed on sandy soil on the coastal plain; the species-rich Atlantic Forest, which reaches its southern limit on the highland slopes [5]; and the highland broadleaved forests, also derived from the Atlantic Forest, with the native Paraná pine Araucaria angustifolia as an emergent canopy species. Based on this profile, we aimed to describe and analyse the diversity of terrestrial isopods (Oniscidea) across local and regional spatial levels, and along a 1000-m altitudinal gradient comprising three distinct environments: the coastal region, the highland slopes, and the highlands themselves.

2. Material and methods

Sampling was done from September 1998 to February 1999 and in September 1999. One-hour-long exploratory manual sampling by the same person was employed at 41 sampling sites: 14 on the highland slopes, 14 on the coastal plain, and 13 in the highlands. Substrates searched included soil, leaf litter, bromeliads, and underneath rocks and logs. The localities sampled predominantly involved native vegetation; we avoided environments altered by humans altogether. Also, no beaches were visited, so beach isopod faunas are excluded from the analysis. Specimens were deposited in the collection of the Departamento de Zoologia of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.

2.1. Study area

The area studied is situated between 29°25′S 50°35′W and 29°21′S 49°44′W, comprising three environments: the coastal plain, highland slopes (locally known as the “Serra Geral”), and highlands (known as the “Planalto Rio-Grandense”).

These environments as described below were characterised according to [9,15] in terms of vegetation and relief. Soil classification used criteria underlined by [11].

The coastal region is composed of dunes, sea terraces, sandy plains, and restinga (a kind of low sclerophyll forest on sandy soils) cordons, where sea and wind action is evident. The plant formations are thus under the influence of the sea, on soils that are not only sandy but have considerable salt content and low natural fertility. The highland slopes are formed of a sequence of predominantly basic volcanic rock with some acidic elements. Plant formations are a type of Atlantic Forest, with clay-like mineral soils and high levels of organic matter, usually considered as potentially arable soils. The uplands are in an area between reliefs sculpted on crystalline rock and others on volcanic rock. Plant cover is defined by the distribution of the native Paraná pine A. angustifolia. The acidic mineral soils are shallow, typical of higher altitudes, with a clay-like texture and rich in organic matter.

2.2. Quantitative analysis

We employed a number of different tools to analyse diversity and abundance patterns of the Oniscidea, including alpha and beta levels of analysis, and analysis of macroecological patterns. Ordinary statistical tests were done using SPSS 11.5; for specific diversity tests we employed the freely available software WS2M [27] and PAS [8]. The alpha analysis (quantitative) included: 1) sampling effort curves, which were plotted and randomised, along with analytical estimates of expected species richness for the entire region; 2) comparisons of abundance, species richness, and diversity among the three environments. Beta analysis (qualitative) considered the similarity of faunas at site and region levels, ubiquity of species and exclusivity of species per environment, and the number of native and introduced species. Macroecological patterns analysed here include altitudinal effects and the relationship between abundance and spatial distribution of species.

3. Results and discussion

Overall, 14 species of Oniscidea were identified, of 818 individuals collected in 41 samples. On average, there were 19.95 individuals and 2.48 species per sample site. There were 2–60 individuals and one to five species per sampling site. A list of the species found and the environments where they were present is shown in Table 1. A total of 32 species of Oniscidea are recorded for the State of Rio Grande do Sul [1,14,16,17]; therefore, in our study we found nearly half of the species known from the entire region.

Comparisons with other studies are difficult, because most are concerned with biogeographic patterns and pro-
vide neither species inventories nor total or local species richness and abundance. One similar study done in the Czech Republic identified 18 species of 14,667 individuals trapped [26]. The study area in the Czech Republic was smaller than ours, but richer in habitats and included urban and rural areas. It would thus seem that our work recorded a comparatively rich assemblage of species.

3.1. Sampling-effort curves

Sampling-effort curves (Fig. 1) stabilised for all the data and for the three environments separately, approximately after half the samples were taken; thus, we are confident that our sampling methods were efficient. Because the curves appeared so clearly asymptotic, we did not try to fit any known mathematical functions. However, Fig. 2 shows a randomised sampling-effort curve for 10,000 runs of sample shuffling without replacement, along with the observed curve. It can be seen that the latter frequently exceeds the estimated curve; that is, species were apparently collected faster than would be expected by chance alone. Stabilising of collector curves is essential in order to reach broad conclusions about the faunas of the different regions.

3.2. Estimating the number of species

Very few invertebrate surveys, especially in the tropics, are exhaustive to the point of recording all species, and asymptotic estimators of species richness are commonly employed [7]. A stabilisation of the accumulation curve was clear in our data, and five out of six species richness estimators returned values effectively identical to the observed richness, although one estimator predicts more species to be found in the region (Table 2). It seems, therefore, that we can expect the recorded species richness to be very close to its true value in nature.

3.3. Abundance

The absolute number of individuals varied from region to region. Because the sampling method was standardised, we judged it reasonable to compare environments in terms of perceived abundances as well as number of species. The coastal environment had the highest abundance (320 individuals), followed by the highlands (282), and the highland slopes (216). However, because our sampling design was unbalanced (see Section 2), conclusions based on raw data would be biased against the highland region, which had one less sampling site than the others. On average, the coastal region and the highlands had more than 20 individuals per sampling site, whilst the slopes had fewer than 16. Although it is indicative of a trend (see below), this difference is not statistically significant (one-way ANOVA, $F_{2,38} = 1.118, P = 0.338$). It seems that the number of oniscideans varies considerably more among

Table 1
List of species of Oniscidea obtained from 41 sampling sites in three different environments of northeastern Rio Grande do Sul, southern Brazil

<table>
<thead>
<tr>
<th></th>
<th>Coastal plains</th>
<th>Highland slopes</th>
<th>Highlands</th>
</tr>
</thead>
<tbody>
<tr>
<td>Armadillidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudodiplöexochus tabularis (Barnard, 1932)</td>
<td>a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ballioniscidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ballioniscus glaber Araujo and Zardo, 1996</td>
<td>b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ballioniscus sellowii (Brandt, 1833)</td>
<td>c</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bathyropyidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neotroponiscus daguerrii (Giambiagi de Calabrese, 1939)</td>
<td>d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dubioniscidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Novamundoniscus gracilis Lopes and Araujo, 2003</td>
<td>e</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Philosciidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alboscia silveirensis Araujo, 1999</td>
<td>f</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atlantoscia floridana (van Name, 1940)</td>
<td>g</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthana picta (Brandt, 1833)</td>
<td>h</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthana serrana Araujo and Lopes, 2003</td>
<td>i</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthana trinodulata Araujo and Lopes, 2003</td>
<td>j</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Benthana araucariana Araujo and Lopes, 2003</td>
<td>k</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Platyarthridae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trichorhina argentina Vandel, 1963</td>
<td>l</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trichorhina sp.</td>
<td>m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Styloiscidae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Styloiscus otakensis (Chilton, 1901)</td>
<td>n</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
3.4. Species richness

Differences among areas in terms of regional species richness reversed the above pattern of abundance (Fig. 3): slopes had a higher number of species (11 of 14), whilst the other two environments had seven species each. At the local level, differences in species richness reached only marginal significance among environments (one-way ANOVA, $F_{2,38} = 3.082, P = 0.057$).

3.5. Abundance/richness relationships and rarefaction

The relationship between the number of individuals sampled and the resulting species richness is usually positive [3]. In our system it seems that this rule was weakly followed ($r^2 = 0.077$) and not at a significant level, although nearly so (regression analysis, $F_{1,39} = 3.259, P = 0.079, N = 41$). This is probably because of the differences found for the highland slopes, where the number of oniscideans sampled was lower, even though more species were found.

We would expect that a rarefaction analysis would confirm our results on the differences in richness of the environments. The overall curve decreases slowly, because of the high dominance of a few species (Fig. 4a). The curve for the richest region (highland slopes, Fig. 4b) actually intersects the latter, whilst the other two are much lower and never intersect the curve for

Table 2

<table>
<thead>
<tr>
<th>Estimator index</th>
<th>$\hat{S}_{est}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bootstrap</td>
<td>14.19</td>
</tr>
<tr>
<td>Chao 1</td>
<td>14.00</td>
</tr>
<tr>
<td>Jackknife</td>
<td>14.03</td>
</tr>
<tr>
<td>Log-normal</td>
<td>14.06</td>
</tr>
<tr>
<td>Michaelis–Menten</td>
<td>16.35</td>
</tr>
</tbody>
</table>
slopes except at the origin. This shows that the highland slopes has a higher regional diversity, that is a higher number of species on a per sampled individual basis.

3.6. Diversity measures

Comparisons of environments based on a single diversity measure are sometimes criticised, because each diversity index evaluates a combination of species richness and evenness weighted differently. These different aspects should be taken into consideration, but there is another way to avoid this problem. There is a general equation that can attribute different weighting to richness and evenness based on a parameter ($\alpha$), generating a “family” of diversity indexes [10]. Constructing a curve based on these values for different $\alpha$, we can directly compare environments in terms of richness, diversity, or dominance. Such a treatment is shown in Fig. 5, where it can be seen that the curves do not cross except at the origin for the coastal plain and highlands (since they have equal species richness). A direct comparison of local diversity among the environments seems, therefore, appropriate, irrespective of the index used.

Because we chose to use Shannon–Wiener’s $H'$, the diversity pattern is a combination of those for abundance and richness: at a regional level, the highland slopes were more diverse (Fig. 6) and the only environment to have an index higher than 1.5 (which is relatively low compared to other taxa [18]). There are two ways of comparing diversity among environments, and we present both. First, bootstrap estimates with confidence intervals (calculated from abundance distribution of species: coastal 0.5629–0.8046, slopes 1.591–1.884, highlands 1.039–1.279) showed these differences to be significant at a regional level. For the local level (one-
way ANOVA with diversity calculated for each sampling site), $H'$ was also significantly different ($F_{2,38} = 6.634, P = 0.003$), with the highland slopes locally more diverse than the coastal environment. However, no other difference was found to be significant by a multiple comparisons test (Tukey’s HSD).

3.7. Beta diversity

By separating beta aspects of diversity, we wish to emphasise the qualitative differences among environments and between sites; that is, to consider species identity directly. An additive partitioning of the diversity found in each environment [28] revealed that alpha (local) richness accounted for only 27–35% of the diversity in each environment, and thus variation among sites was responsible for two-thirds or more of the diversity. This seems to show that the sites differed considerably in their composition, even within a relatively homogeneous environment. Partitioning, taking the level above into consideration, reduced the importance of local richness to 19% of the total richness, with local beta diversity (differences among sites within regions) contributing 42% of the total richness, and regional beta diversity (differences among regions) 39%.

Only two species were “universal”, that is, occurred in all three environments: Atlantoscia floridana (van Name, 1940) and Balloniscus glaber Araujo and Zardo, 1996 (Fig. 7). These were also two of the three most abundant species, accounting for 72.7% of all individuals caught (Fig. 8). There were five species exclusive to only one environment, three on the highland slopes and one in each of the other environments (see Fig. 7 for details); also, only three species did not occur on the highland slopes. This lends more weight to the conclusion that highland slopes are more diverse than the other environments. The single species exclusive to the coastal environment, Pseudodiploexochus tabularis (Barnard, 1932), is probably introduced, since it is native to South Africa [6]. The coastal plain and the highlands share only one species, which is not surprising because they are usually not contiguous ecosystems. This may also be the reason why the highland slopes share three species with each of the other environments.

Similarities among environments in terms of the species and abundance are shown in Table 3. Above the middle line we give the Raup–Crick index for presence–absence data, and below, the Morisita index for abundance. It can be seen that the coastal and highland ecosystems are more similar although they are spatially disjunct. This probably has to do with the higher species richness of the highland slopes, also qualitatively separating them from the others. An ANOSIM analysis with Morisita’s similarity index returned a significant
result: the environments varied more between each other than within themselves (mean rank within = 369.5, mean rank between = 429.5, \( R = 0.146 \), \( P < 0.001 \)); an equivalent result was found with the presence–absence Raup–Crick index. However, cluster analysis (not shown) for similarity of composition of sampling sites revealed no consistent pattern. None of the higher-order clusters (less than 0.8) joined points from a single environment only, demonstrating a low similarity among sites at the local level.

### 3.8. Macroecology: frequency adequately estimates abundance

The relationship between frequency per sampling site (presence/absence) and total abundance was highly significant when all species were considered (Pearson correlation, \( r^2 = 0.942 \), \( P < 0.001 \)). However, because \( A. floridana \) was both more abundant and more frequent than the others, it could be driving the pattern. When this species was omitted from the analysis, the relationship, though weaker, was still significant (\( r^2 = 0.562 \), \( P = 0.003 \)). Thus, the spatial distribution of each species, as judged by the number of sites occupied, was correlated with its abundance in the same region, following the classic macroecological pattern of wider distribution associated with higher abundance [2]. This also revealed frequency as an interesting alternative estimate for relative abundance that would be easier and faster to assess than total counts, if identification is possible in the field. A similar result (locally rare species are never widespread), although using a different method of analysis, was found for Greek terrestrial isopods [22].

### 3.9. Altitudinal gradient

Because the sites are distributed along an altitudinal gradient from the coast, nearly at sea level, to the highlands, at 1000 m altitude, it seemed appropriate to evaluate the effect this has on the diversity of the Oniscidea. The linear regression was nearly significant \( (F_{1,39} = 3.379, \ P = 0.074) \), but its explanatory power was very low \( (r^2 = 0.080) \). A second order polynomial was highly significant \( (y = -3 \times 10^{-6}x^2 + 0.0028x + 0.3506, F_{2,38} = 9.535, \ P < 0.001) \) and had good explanatory power \( (r^2 = 0.334) \), providing the best fit for the relationship (Fig. 9). This was to be expected, because the highland slopes are more diverse in many respects and are situated between the coast and the highlands. Local species (that is, richness per sampling point) does not show a curvilinear trend as diversity does, although regional richness is higher for the highland slopes than for the extreme regions (coastal plains at the lowest altitudes and highlands at the highest altitudes). The reasons behind this may be mathematical; since there are very few species per sampling point (two or three), and thus actual differences from point to point are too slight to be significant.

Previous work on altitudinal gradients and oniscidean diversity has shown that species richness tends

![Fig. 9. Altitudinal gradient in oniscidean diversity across 1000 m, with altitude above sea level plotted against the Shannon diversity index per sampling site. A first-order polynomial regression fitted the relationship significantly (see text).](image-url)
to decrease with altitude in the mountains of Greece [19], although for intermediate altitudes in Israel (400–600 m), species richness was higher than for coastal areas [29]. In our study, firstly, the highlands are not high enough to generate marked differences in climatic conditions; secondly, the increase in altitude is not towards isolated mountaintops, but to the edges of a vast upland region. Thus, we would not expect abrupt changes in the fauna along this altitudinal gradient, both because temperature and humidity do not differ much (although the soil does), and because a “reduced area” effect (for more or less conical mountains, there is less surface area as altitude increases, and thus diversity decreases as a species-area effect [13]) should not apply. The highland slopes are thus a biogeographical contact zone between the coastal and highland environments, and should be expected to harbour more species, as they do.

4. Conclusion

Oniscideans are important players in soil ecology and a useful tool in diversity studies. Because they do not form particularly species-rich assemblages, it appears that reliable estimates for diversity and its components can be derived, and patterns interpreted.

The overall picture emerging from our sampling is that there is considerable heterogeneity at the local level in terms of species richness, diversity, and composition. Alpha diversity made a small contribution to total diversity. This may reflect the sampling regime in which a degree of subjectivity is inherent; perhaps the use of traps or an increase in the time allocated to searching could prevent that. Nevertheless, we trust that our results are robust, because the asymptotic sampling-effort curves and species-richness estimates demonstrated the completeness of the study.

In spite of variation among sites, patterns at the regional level could be detected, and differences in species richness, diversity, and composition among the three regions studied were evident: although they seemed to have lower abundance, the highland slopes had more species, more exclusive species, and higher local and regional diversity.

An explanation for this pattern may be sought in the biogeographic status of the highland slopes. A hump-shaped pattern appeared in the altitudinal gradient. The proposed scenario of a contact zone between two regions (coastal and highland) would lead us to expect a curvilinear pattern in terms of alpha diversity (more species in the “contact” zone). The coastal and highland assemblages of oniscideans, however, are more similar to each other than to the highland-slope assemblages (beta diversity), exactly the opposite that we would expect. Therefore, this biogeographical explanation is not warranted. An alternative hypothesis may be that some specific environmental characteristic of the highland slopes is more important for the coexistence or colonisation of oniscidean species. One obvious candidate could be the inclination of the terrain, and its effect on the quality, quantity and dynamics of leaf litter, and soil characteristics. Soils of the coastal region are sandy and relatively poor, whilst the highlands have acidic soils. A negative effect of salinity on the species richness of terrestrial arthropods in coastal areas in France has been documented [4]. In UK, areas of acidic and swampy soils have low oniscidean abundance and diversity [24]. It appears that soil type may be an alternative explanation for our results. At any rate, more data on the biology of the species and an extension of sampling to other comparable places would also add significantly to our understanding of the problem of the origin and maintenance of diversity in assemblages of Oniscidea.

Acknowledgements

We would like to acknowledge CAPES for scholarships to the first and second authors and to PPG-Biologia Animal-UFRGS. This is contribution No. 455 of the Departamento de Zoologia.

References
