Relative effects of biotic and abiotic factors on the composition of soil invertebrate communities in an Amazonian savanna

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Abstract

Using ordinations techniques, we investigated the effects of different types of plant cover on the relationship between soil structure and invertebrate communities in an Amazonian savanna. Vegetation islands were chosen where four selected shrubs species were present on sandy and clayey soils. For each sample under a selected shrub within the clump, another sample was taken in the grass-tuft and extracted in Berlese-Tullgren. Classifying at higher taxonomic levels, we detected 27 zoological categories. The mean number of individuals was generally higher on shrubs. Acari and Collembola were the dominant groups. Non-Oribatid mites dominated in the savanna, in contrary with what occurs in most Amazonian ecosystems, where the dominance of Oribatida is always higher than others Acari. The level of taxonomic resolution utilized was sufficient to show the main differences of the spatial variation in community structure. We detected effects of soil type, vegetation structure and plant specie identity on the composition of the communities. The mesofauna have a mosaic distribution in the savanna dependent on the soil-food web structure of the vegetation. Shrubs and grass-tuft generate different ecosystems. Therefore, studies with better taxonomic resolution will be necessary to assess the magnitude of the effect of biotic and abiotic factors.
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1. Introduction

In Amazonia, edaphic organisms such as invertebrates, roots, and microflora play an important, if not predominant, role in soil structural organization, both by forming and destroying aggregates and altering their assemblage in the profile (Barros et al., 2004). It is to be expected that soils of different structure and vegetational cover will harbor different communities of soil invertebrates (Abbott et al., 1979; Majer, 1989). However, it is time consuming and expensive to identify these invertebrates to specie level. The proportion of 'morphospecies' that cannot be assigned to named species and the number of 'scientist-hours' required to process samples both increase dramatically for smaller-bodied taxa (Lawton et al., 1998), that

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compose the majority of the soil mesofauna groups. In a complex and poorly studied region, such as Amazonia, even groups that are widely used in environmental studies (e.g. Oligochaeta, ants and termites) are far from being taxonomically well known.

The concept of taxonomic sufficiency (TS; Ellis, 1985), involves the identification of organisms only to a level of taxonomic resolution sufficient to satisfy the objective of a study (Pik et al., 1999; Terlizzi et al., 2003). Unfortunately, taxonomic sufficiency for detecting habitat-related changes in invertebrate communities in Amazonia is unknown. Most studies have used classification at the level of class, order or family (e.g.: Adis et al., 1987; Adis, 1988; Oliveira and Franklin, 1993; Vohland and Schroth, 1999; Franklin et al., 2001). Within pure taxonomic levels, zoological components can be separated according to stage of development (adult/immature) or the main feeding habit of the individuals (Moore et al., 1988). In Amazonian ecosystems, several studies have used functional zoological groups (e.g. Franklin et al., 2001; Höfer et al., 2001; Barros et al., 2002, 2004) to investigate factors affecting the distribution of soil invertebrates. In Western Amazonia, there is evidence that soil macrofauna classified at higher taxonomic level, and using principal components analysis, can show effects of land-use (Barros et al., 2002).

We used the natural variation in soil and plant cover in an Amazonian savanna to investigate the effects of different types of plant cover on the relationship between mineral soil structure and invertebrate community composition. We also investigated whether soil invertebrates at the savanna show consistent pattern in distribution when analyzed at high levels of taxonomic sufficiency. The Amazonian-type savannas (Huber, 1982) of northern Brazil have low floristic diversity (Miranda, 1993, 1995) and most of them are burned frequently at the end of the dry season (September–October). This affects the floristic diversity and composition of the ecosystem, because grasses and shrubs form functional groups that differ in their responses to external factors such as fire (Ginoux et al., 1996; Jeltsch et al., 1998). These groups also differ in their effects on soil structures, principally because of differences in inputs of organic matter. Soil percent material may also affect vegetation structure. Sandy and clayey soils differ sharply in

structure, water relationship and nutrient retention and availability (Brady, 1989). Two types of soil occur within the savanna at Alter do Chão. The most common is a loose sandy soil, with yellowish surface that becomes darker with depth. However, nearby a less sandy and darker soil can be found a more clayey and compact soil. However, the vegetation cover is broadly similar and many shrub species occur on both types of soil. It is not clear to what extent the vegetation cover can modify the effects of the mineral fraction of the soil on invertebrate communities.

We initially investigate the effects of vegetation type (shrubs or grass-tuft) and soil type (clayey and sandy) on the structure of the invertebrate community. We then test for differences among species of shrubs for their effects on mesofauna communities under the shrubs and in the surrounding grass-tuft matrix. For biological reasons, and consideration of previous studies, it is unlikely that any of the hypotheses we present here are false. That is, soil type, vegetation structure, and vegetation species composition almost certainly affect the invertebrate community to some extent. However, the relative magnitude of these effects is unclear and it is not known to what extent the biotic factors can compensate for variation in mineral soil structure. Management of savanna areas usually implies management of vegetation structure and composition, but it is unclear whether management practices designed to maintain the conservation value of the vegetation would be of equal benefit to the invertebrate community (Sanderson et al., 1995). If the taxonomic resolution used in most studies in Amazonia is not sufficient to detect natural variation in soil invertebrate's communities, it is unlikely to be adequate to detect subtle effects caused by human interventions.

We used ordination techniques to locate zoological categories in multivariate space based on similarities in their occupation of sites. If organisms in different categories do not differ in spatial distribution, they will be poor indicators of spatial variation in community structure. We identified the invertebrates in taxonomical levels of class, sub-class, order, sub-order or family, and then in zoological categories, according to their main feeding habit and/or stage of development. We divided the zoological categories in two groups: all-invertebrate community and non-mite, non-collembolan invertebrate community. We hypothesized that: (1)

the soil type affects the mesofauna communities; (2) the mesofauna communities under shrubs are different from those under grass-tuft; (3) the species of the shrub affects the invertebrate communities, and this effect could override differences due to mineral soil; (4) taxonomic resolution in higher zoological categories is sufficient to detect changes in soil invertebrates due to natural variation in soil and vegetation structure.

2. Methods

The study was carried out in two savanna sites, separated from each other by 1 km, one with sandy soil and the other with clayey soil, situated on the right margin of the Tapajós river, near the village of Alter do Chão (2°31′S and 55°00′W), in the state of Pará. The climate is Ami (tropical wet) in the Köppen classification, with a well-defined dry season, mean annual rainfall of 1950 mm, with 75% of the rain falling between December and June. The dry season extends from June to December. The mean annual temperature is 27.7 °C and the mean monthly temperature varies less than 1.5 °C from the annual mean (Miranda, 1993).

The vegetation in the areas surveyed is dominated by an herbaceous stratum composed principally of the tufts forming grasses *Paspalum carinatum* and *Trachypogon plumosus*, interspersed with patches of trees and shrubs. Regular semi-annual burning can drastically reduce the area covered by the common shrub species of the genera *Miconia* and *Myrcia*, and the area made available by the loss of the shrubs may be occupied mainly by the grass *P. carinatum* (Sanaiotti and Magnusson, 1995). The stature of trees is short, and many have tortuous trunks, thick cortex and leathery leaves. Trees do not form a continuous canopy and, in the area we studied, the vegetation is grouped into well-defined clumps, consisting of trees, shrubs or herbs. Tracts of grass, dominated by *P. carinatum* mixed with sedges and other herbaceous plants, occur between clumps of shrubs (Miranda, 1993).

Soil characteristics differed sharply under shrubs and grass tufts in the clayey but not in the loose sandy soil. Under clayey soil, the clay content under shrubs (17.7 ± 2.1, $n = 3$) was higher than under grass-tuft (5.9 ± 1.4, $n = 5$). A higher C concentration was

detected under shrubs (2.5 ± 0.2, $n = 3$) in relation to grass-tuft (1.6 ± 0.7, $n = 5$). These difference were significant at 5% two sample *t*-test ($p = 0.003$ and $p = 0.042$, respectively). Under loose sandy soil, the clay percentage under shrubs (6.2 ± 1.7, $n = 4$) did not differ from the value obtained under grass-tuft (4.3 ± 1.2, $n = 4$). No difference was detected comparing the value for C concentration (1.9 ± 0.6, $n = 4$ under shrubs; 1.8 ± 0.4, $n = 4$ under grass-tuft).

The samples were taken between 28 and 30 August 1996, during the dry season. At each savanna site, on sandy and clayey soils, we chose those vegetation islands where four shrubs species [*Myrcia sylvatica* (Meyer) DC, *Miconia albicans* (Sw.) Triana, *Manihot caerulenscens* Pohl subsp. Paraensis (Mueller von Argau) Rogers & App and *Chomelia ribesioides* Benth. Ex M. Arg.] were present. Twelve shrubs on each soil type were sampled, giving three repetitions for each shrub species on each soil, totalizing 24 samples under shrubs. For each sample under a selected shrub within the clump, another sample was taken outside the clump, in the grass-tuft matrix, totalizing 24 samples under grass-tuft. Samples were taken using a 49 cm^2 metal corer, introduced to a depth of 5 cm into the soil. The sampled area covered at each shrub and each grass-tuft was 0.0025 m^2.

In the same day as collection, the samples were prepared for extraction with Berlese-Tullgren extractor, in a local laboratory. We used 1% formaldehyde solution as a collector liquid. The samples were extracted during 6–7 days, during which time the temperature of the extractor was raised slowly from 28 to 45 °C.

We identified the invertebrates in taxonomic levels of class, sub-class, order, sub-order or family. Our method was not efficient at catching Nematoda, Enchytraeidae (microfauna) and invertebrates larger than 2 mm (macrofauna), and these were not included in analyses. Within taxonomic levels, we classified the individuals in zoological groups, according to their main feeding habit and/or stage of development (adult/immature). Acari was separated into zoological groups of Oribatida (80–85% detritivorous species), and Acari Non-Oribatida, the majority being predators. Diptera, Coleoptera, Homoptera, Hemiptera and Thysanoptera were separated into adults and immatures, because of the great differences in feeding habits. Hymenoptera were separated into ants and

other groups. Twenty-seven faunal community variables (zoological categories) were found.

We used ordination to summarize the major pattern in the data. Ordinations were undertaken in the non-metric hybrid multidimensional scaling (SSH-MDS) module of the PATN Program (Belbin, 1992). The apriori decision was made to use two dimensions (SSH1 and SSH2), to capture the major gradients. Minor patterns may exist in other dimensions, but they are difficult to interpret (Gauch, 1982), and we did not have sufficient repetitions to justify such analysis.

The ordinations were undertaken for quantitative and for qualitative (presence/absence) data. The quantitative data were transformed by dividing taxonomic groups by the sum of squares to balance the contribution of rare and common taxa. Data in sites were divided by site totals to give the same weight to each site. We made the ordinations for two groupings: all-invertebrate community and, the non-mite, non-collembolan invertebrate community. The ordinations based on qualitative data (presence/absence) give more weight to uncommon species, as common species tended to occur in most sites, and therefore contributed little to qualitative differences among sites. The Bray Curtis Association Index was used to indicate the dissimilarity between the samples. When used on presence/absence data, this association is called the Sorensen index. Ordination with MDS and the Bray Curtis distance is generally effective at detecting ecological gradients (Kenckel and Orloci, 1986; Minchin, 1987). The MDS axes are linear and approximately orthogonal and therefore conform to the principal assumptions of multivariate analysis of variance (Anderson and Legendre, 1999).

A measure of 'stress' and r^2 statistic was calculated. Stress is a mismatch between the rank order of distances in the data, and the rank order of distances in the ordination (the higher the value, closer are the implied ultrametric-distances from the dendrogram to the input association measure). The r^2 statistic is descriptive of the proportion of the variance in the original distances captured by the ordination and is generally comparable among analyses, though it may slightly underestimate the effectiveness of the MDS, which does not require a linear relationship between the input and output distances.

Ordinations summarize the major pattern in the data and may not capture patterns in subgroups well. Therefore, we conducted ordinations of sites for samples under shrubs and grasses together, and then separately to investigate the effects of shrub type. We used MANOVA to test for the effects of (1) soil type (clayey or sandy), (2) structure of the vegetation (the environment under shrubs clumps, or under grass-tuft) and (3) shrub species (*M. sylvatica*, *M. albicans*, *M. caerulescens* and *C. ribesioides*). It is probable that any change will have some effect on some invertebrate species. We investigated only the effects of the independent variables on the major patterns of the community, that is, those captured by the two dimensions of the ordination.

3. Results

3.1. The invertebrate fauna of the savannas

Twenty-seven zoological categories were detected in both savannas. Chilopoda, adults Homoptera, and Phalangida were not found in the savanna on clayey soil. Immatures and adults Diptera, immatures Lepidoptera, Pauropoda, Symphyla, and immatures Thysanoptera were not found in the savanna on sandy soil. The mean number of individuals was generally higher on shrubs (28.3–240.3 individuals) than on grass-tufts (9.0–106.3 individuals).

The highest invertebrate density was detected under *M. sylvatica* shrubs, caused by the high density of Acari Oribatida, resulting from a great dominance of *Rostrozetes foveolatus* Sellnick, 1925, in both soil types. Acari Oribatida, Acari Non-Oribatida and Collembola were dominant in all of the sites sampled, representing more than 60% in relation to the total invertebrate fauna. In the savanna, greatest dominance of Acari Non-Oribatida was characteristic of the grass cover and of the schrubs, with exception of *C. ribesioides* on the clayey and sandy soil, and *M. silvatica* on sandy soil. Collembola was more dominant in the savanna on clayey soil (Appendix A; Table 1). For simple comparison, the results for a primary forest were included in Table 1.

3.2. All-invertebrate community—soil, shrub species and vegetation structure

Multivariate multiple regression for quantitative data indicated no statistically significant effect of soil

Table 1
Relative dominance of Acari Oribatida, Acari Non-Oribatida, Collembola, and non-mite, non-collembolan invertebrates in relation to the total catch in the soil and litter layers of a primary forest and Amazonian-type savanna areas of Alter do Chão. Pará. Brazil

		Acari		Collembola	Non-mite, non-collembolan invertebrates
		Oribatida	Non-Oribatida		
Primary forest (clayey soil)		58	20	2.4	19.6
Savanna (clayey soil)					
M. sylvatica	S	26	63	3	8
	G	27	61	0.3	11.7
M. albicans	S	27	43	9	21
	G	35	53	0	12
M. caerulenscens	S	30	49	3	18
	G	32	55	0.5	12.5
C. ribesioides	S	45	44	1	10
	G	14	82	0	4
Savanna (sandy soil)					
M. sylvatica	S	55	14	16	15
	G	23	33	6	38
M. albicans	S	30	51	10	9
	G	17	59	0	24
M. caerulenscens	S	29	34	15	22
	G	17	69	2	12
C. ribesioides	S	44	35	10	11
	G	18	65	5	12

S = shrub; G = grass-tuft.

(Pillai trace = 0.059; $P = 0.312$) or shrub species (Pillai trace = 0.211; $P = 0.178$). However, community was affected by the structure of the vegetation (MANOVA; Pillai trace = 0.422; $P = 0.000$). The variation was principally on the MDS axis 1 (ANOVA, $P < 0.001$). The all-invertebrate community under shrubs was distinct from that in the grass-tuft matrix. The ordination (stress: 0.238, $r^2 = 0.856$) showed the separation of the samples into shrub and grass-tuft communities (Fig. 1A).

Multivariate multiple regression for qualitative data indicated no statistically significant effect of soil (Pillai trace = 0.934; $P = 0.275$) or shrub species (Pillai trace = 0.160; $P = 0.354$). However, the community was affected by the structure of the vegetation (MANOVA; Pillai trace = 0.355; $P = 0.000$). The variation was principally on axis 2 (ANOVA, $P < 0.000$). The ordination (Fig. 1B; stress: 0.267, $r^2 = 0.783$) indicated significant separation of the samples into shrub and grass-tuft communities.

Plots of relative frequency of the zoological categories of invertebrates against the sampling sites (24 under shrubs and 24 under grass-tuft) reflect different groups according to the structure of the vegetation (Fig. 2). One group consists of generalists, such as Acari Non-Oribatida, Acari Oribatida and immatures Homoptera, which occurred under both shrubs and grass-tuft. Some small groups, such as Psocoptera and immatures Diptera grouped to the lower left of Fig. 2, occurred mainly under grass-tuft. Taxa in the upper right of Fig. 2, such as Araneae, Coleoptera immatures, Diplura, Pseudoscorpionida, Collembola, adults Coleoptera, Isopoda and Protura, occurred mainly under shrubs. Other taxa were rare and no association with vegetation cover can be inferred.

3.3. All-invertebrate community under shrubs—soil and shrub species

Multivariate multiple regression for quantitative data indicated no statistically significant effect of shrub specie (Pillai trace = 0.294; $P = 0.386$). However, the community was affected by the soil type (MANOVA; Pillai trace = 0.296; $P = 0.043$). The variation was principally on the MDS axis 1 (ANOVA, $P < 0.015$). The ordination (stress: 0.214; $r^2 = 0.888$) shows clear separation of the samples from clayey and sandy soils (Fig. 3).
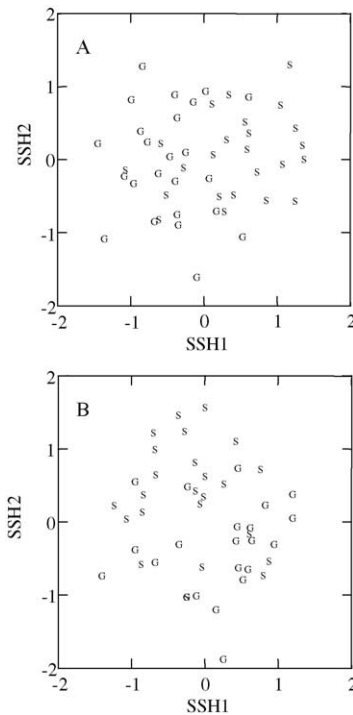
Fig. 1. Ordination in two dimensions by hybrid multidimensional scaling (SSH) of the total invertebrate community collected under shrub and grass for (A) quantitative data, and (B) qualitative data. S = shrub, G = grass tufts.
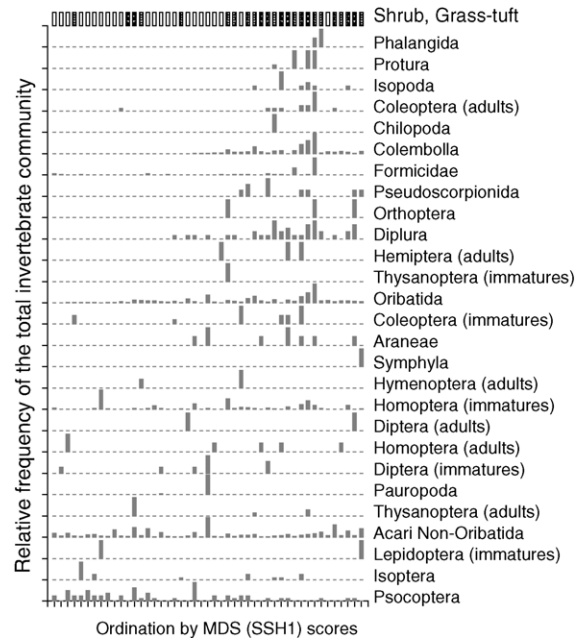

Fig. 2. Upper panel indicates whether the sample was taken under shrubs (solid bars) or under grass tufts (open bars). Gray bars indicate the relative frequency of each zoological category within all-invertebrate community. Sites are ordered by their position on axis 1 of an MDS ordination (see text).

For qualitative data, the invertebrate composition under shrubs was not significantly affected by shrub specie (MANOVA; Pillai trace = 0.233; $P = 0.551$) or soil type (MANOVA; Pillai trace = 0.250; $P = 0.075$). However, for the soil, the low probability of the null hypothesis and a significant difference on axis 2 (ANOVA, $P < 0.028$) in individual analyses of each axis indicate a possible type II error (the probability of accepting the null hypothesis when it is false).

Plots of relative frequency of the zoological categories of invertebrates against the soil type (12 samples under clay soil and 12 samples under sandy soil) indicate different responses among taxa to soil type (Fig. 4). One group consists of generalists such as Acari Non-Oribatida, Acari Oribatida and Diplura, which occurred on both clayey and sandy soil. A second group including Pseudoscorpionida and Psocoptera, joined in the lower left of Fig. 4, were more frequent on clayey soil. The third

group, in the upper right, such as Isoptera, Collembola, adults and immatures Coleoptera, and Isoptera, were more frequent on sandy soil. Other taxa were rare and no association with soil type can be inferred.
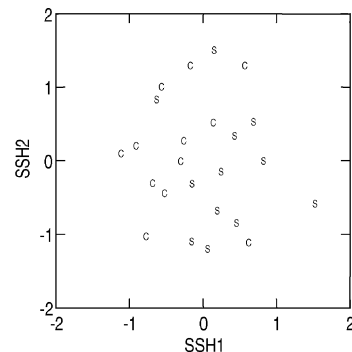

Fig. 3. Ordination in two dimensions by hybrid multidimensional scaling (SSH) of all-invertebrate community collected under shrubs for quantitative data. C = clayey soil, S = sandy soil.
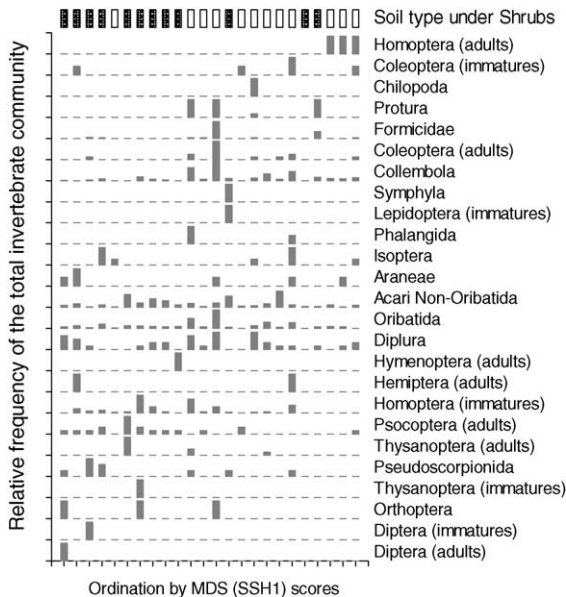
Fig. 4. Upper panel indicates whether the sample was taken on clayey soil (solid bars) or sandy soil (open bars). Gray bars indicate the relative frequency of each zoological category within all-invertebrate community. Sites are ordered by their position on axis 1 of an MDS ordination (see text).
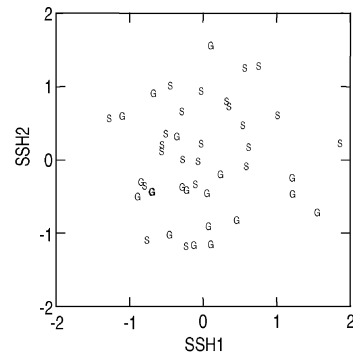

Fig. 5. Ordination in two dimensions by hybrid multidimensional scaling (SSH) of the non-mite, non-collembolan invertebrates collected under shrubs and grass tufts for qualitative data. S = shrub, G = grass-tuft.

3.4. All-invertebrate community under grass-tuft—soil type and shrub species

Multivariate multiple regression for quantitative data indicated no statistically significant effect of shrub specie (Pillai trace = 0.299; $P = 0.374$) and soil (Pillai trace = 0.183; $P = 0.163$). However, for soil type the variation on the MDS axis 2 (ANOVA, $P < 0.058$) was very close to the established significance limit.

For qualitative data, the ordination was not significantly related to soil (MANOVA; Pillai trace = 0.115; $P = 0.332$) or shrub species (MANOVA; Pillai trace = 0.267; P = 0.456).

3.5. Non-mite, non-collembolan invertebrate community—soil, vegetation structure and shrub species

For quantitative data, the ordination of all samples (24 under shrubs and 24 under grass-tuft) was not statistically significantly affected by the vegetation structure (MANOVA; Pillai trace = 0.149; $P = 0.070$). However, the low probability of the null hypothesis

and a significant difference on MDS axis 2 (ANOVA, $P < 0.021$) in individual analyses of axes indicates a possible type II error. The community was also not statistically significantly affected by the plant species (MANOVA; Pillai trace = 0.257; $P = 0.142$) but the significant differences on MDS axis 2 (ANOVA, $P < 0.042$) in individual analyses of each axis also indicates a possible type II error. The community was not affected by the soil (MANOVA; Pillai trace = 0.081; $P = 0.247$).

For qualitative data, the community was not affected by the soil (MANOVA; Pillai trace = 0.117; $P = 0.128$) or by shrub species (MANOVA; Pillai trace = 0.180; $P = 0.359$). However, an effect of the vegetation structure was detected (MANOVA; Pillai trace = 0.211; $P = 0.020$). The variation was principally on axis 2 (ANOVA, P < 0.005). The ordination axes explained much of the variation in the original data (stress: 0.284, $r^2 = 0.6$) and shows samples collected under shrubs different from those collected under grass-tuft (Fig. 5).

Plots of relative frequency of the zoological categories of invertebrates along the MDS axis 1 reflect their tendency to occur under shrub or grass-tuft (Fig. 6). Psocoptera and Homoptera immatures occurred under both shrub and grass-tuft. Grouped in the lower left of Fig. 6, such as Isoptera, immatures Coleoptera and adults Hemiptera, were more frequent under shrubs. The third group, in the upper right, such as Pseudoscorpionida, Diplura, adults Coleoptera, Protura, and Araneae were more frequent on sandy soil. Other taxa were rare and no association with vegetation cover can be inferred.
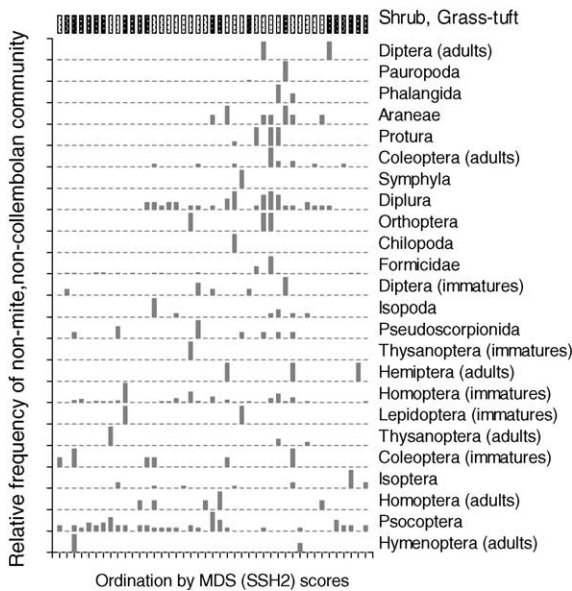
Fig. 6. Upper panel indicates whether the sample was taken under shrubs (solid bars) or grass-tuft (open bars). Gray bars indicate the relative frequency of each zoological category within the non-mite, non-collembolan invertebrates community. Sites are ordered by their position on axis 2 of an MDS ordination (see text).

3.6. Non-mite, non-collembolan invertebrate community under shrubs—soil and shrub species

Multivariate multiple regression for quantitative data indicated no statistically significant effect of soil (Pillai trace = 0.173; $P = 0.198$). The ordination (stress: 0.230; $r^2 = 0.679$) was also not significantly affected by the shrub specie (MANOVA; Pillai trace = 0.540; $P = 0.064$). However, the low probability for the overall null hypothesis and the significant difference on MDS axis 2 (ANOVA, $P < 0.039$) in individual analyses of each axis indicates a possible type II error.

Multivariate multiple regression for qualitative data indicated no significant effect of shrubs (Pillai trace = 0.466; $P = 0.122$). However, there was a significant effect of the soil (MANOVA; Pillai trace = 0.339; $P = 0.030$). The variation (ANOVA, $P < 0.013$) was principally on MDS axis 1 (Fig. 7).

Plots of relative frequency of the zoological categories of invertebrates against the soil type reflect their preferences for the type of soil (Fig. 8). In the upper right of Fig. 8 are grouped those taxa, such as
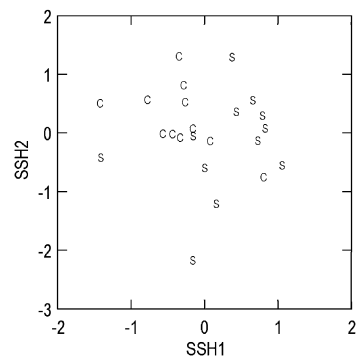
Fig. 7. Ordination in two dimensions by hybrid multidimensional scaling (SSH) of the non-mite, non-collembolan invertebrate sampled under shrubs for qualitative data. C = clayey soil; S = sandy soil.

Diplura, adults Homoptera, Isopoda and adults Coleoptera, that occurred mostly on sandy soils. Another group, such as Psocoptera and Pseudoscorpionida, were more frequent on clayey soils. Other taxa were rare and no association with soil type can be inferred.

Fig. 8. Upper panel indicates whether the sample was taken on clayey soil (solid bars) or sandy soil (open bars). Gray bars indicate the relative frequency of each zoological category within the non-mite, non-collembolan community. Sites are ordered by their position on axis 1 of an MDS ordination (see text).

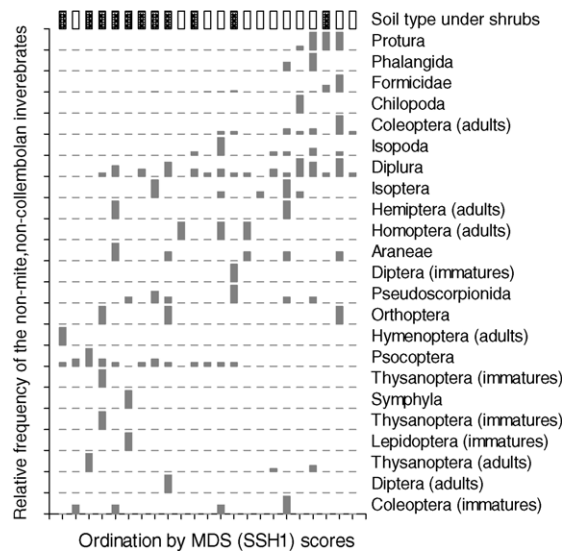### 3.7. Non-mite, non-collembolan invertebrate community under grass-tuft—soil and shrub species

The ordinations of the community sampled under grass-tuft (24 samples) were not affected by any of the factors analyzed (soil and species of shrub). For quantitative data, the ordination was not significantly related to soil (MANOVA; Pillai trace = 0.242; $P = 0.144$) or shrub species (MANOVA; Pillai trace = 0.428; $P = 0.262$).

The ordination based on qualitative data was not significantly related to soil (MANOVA; Pillai trace = 0.157; $P = 0.302$) or shrub species (MANOVA; Pillai trace = 0.201; $P = 0.760$).

4. Discussion

4.1. Density and diversity of the zoological groups

The zoological diversity in the savanna areas was lower compared to an adjacent forest, where we registered 32 zoological categories (Franklin, E.; data not published). The higher concentration of Acari Oribatida, specially *R. foveolatus*, and Non-Oribatida caused the difference between the total sampled under shrubs of *Mycia silvativa*. In Venezuela (South America), a reduction of the diversity and abundance of soil invertebrates from the forest to savanna was detected (Rapoport, 1970). In Amazonia some evidence that the vegetation structure had a strong influence on animals through modification of micro-climate was already detected. In Central Amazonia, the conversion of forest into policulture reduced the diversity, the density and the biomass of meso- and macrofauna (Höfer et al., 2001). In western Amazonia, a reduction of the macro-invertebrate diversity and biomass of pasture in relation to forest was demonstrated (Barros et al., 2004).

In our study, the dominance pattern of Acari in relation to the total catch is similar to reports for other forest environments in Central Amazonia like flooded forest of "várzea" and "igapó", primary and secondary forest and "campinarana" (Franklin et al., 1997). Therefore, in most of Amazonian ecosystems the dominance of Oribatida (46–88%) is greater than other mite groups (Franklin et al., 1997). However, in the savanna soils, the Non-Oribatida, mostly composed of predators, were dominant in relation to the total of Acari. Our results are comparable to those observed in other environments with harsh ecological conditions. In African (Zaire) forests and savannas the Oribatid mites represent 49.4% and 26% of the arthropods, respectively. A reverse gradient is observed in Actinedida that represents 21.5% and 44.1%, respectively, in the two types of vegetation (Noti et al., 1996). In Chilean steppe soil under xerophyllous associations, Trombidiforme (Non-Oribatid mite) is more abundant than the Oribatida (Di Castri, 1963). In the Chihuahuan desert (USA), Acari were dominated by the Prostigmata with the Oribatida making up a smaller percentage of the assemblage. The dominance of Prostigmatids seems to be related to the harshness of the environment (Santos et al., 1978). In burned savannas in Africa (Ivory Cost), the relative abundance of decomposers (principally Oribatida and Collembola) is lower in the unshaded soil that is impoverished of litter and organic matter due to fire and the density of predatory and phytophagous microarthropods is relatively higher (Athias, 1976).

For better understanding of the following discussion, the ordinations of the communities are summarized bellow (Table 2).

4.2. The effect of the soil on the invertebrate communities

Analyzing the samples taken under shrubs and grass-tuft, and on both soil types, the soil did not have a detectable influence on the soil invertebrates. However, removing the effect of the structure of the vegetation and analyzing the samples taken only under shrubs, the effect of the soil type was strong, and it was detected in the all-invertebrate community for quantitative data. There was a similar trend for qualitative data. We also detected the effect for the non-mite, non-collembolan invertebrate for the qualitative data, with a strong trend also for the quantitative data. The all-invertebrate community, composed by less numerically dominant groups, mostly larger than 2 mm, is more mobile and occurs in higher densities in the vegetation layer. The shrubs in the savanna provide a deeper litter layer that enhances water retention as well as moderating soil temperatures. Both factors can favor growth of mesofauna populations. According to Kieft et al.

Table 2
Quantitative and qualitative significant results of the ordinations between the invertebrates and structure of the vegetation (shrubs, grass-tuft), soil type (sandy, clayey), plant species (*M. sylvatica*, *Micornia albicans*, *M. caerulenscens*, *C. ribesioides*), and plant species + structure of the vegetation in Amazonian-type savanna areas of Alter do Chão. Pará. Brazil

	Structure	Soil	Plant	Plant + structure
Shrubs + grass-tuft				
All invertebrates community	Quantitative–qualitative			
Non-mite, non-collembolan invertebrate community	Quantitative (?)–qualitative			
Shrubs				
All invertebrates community	–	Quantitative–qualitative (?)		–
Non-mite, non-collembolan invertebrate community	–	Quantitative (?)–Qualitative		–
Grass-tuft				
All invertebrates community	–			–
Non-mite, non-collembolan invertebrate community	–			–

? = possible type II error; – = not compared.

(1998), plant communities of large portions of the southwestern United States have changed from grassland to desert scrubland and studies have demonstrated that soil nutrient resources become spatially more heterogeneous and are redistributed into islands of fertility with the shift in vegetation. Within adjacent grassland and creosote bush sites, the soils under plants at both sites had greater total and available nutrient resources, with higher concentration under creosote bush than under grass-tuft.

Under the more exposed grass-tuft cover, where the plant diversity was drastically lower, only the community composed of non-mite, non-collembolan invertebrate demonstrated a probable difference in relation to the soil type. Here, we failed to find any relationship of soil type with the all-invertebrate community. These results probably reflect the more adverse conditions of the habitat in the sandy soil, more exposed to abiotic factors, and lower plant diversity that is associated with a low organic content in the soil caused by the thin litter layer.

4.3. Differences between the invertebrate communities under clumps of shrubs and grass-tuft

The effect of the structure of the vegetation was evident, affecting the all-invertebrate community and the non-mite and non-collembolan community. These results showed that the mesofauna have a mosaic distribution in the savanna dependent on the soil-food web structure of the vegetation (shrubs and grass-tuft). In this case, shrubs and grass-tuft appear to generate different ecosystems in the savanna areas of Alter do Chão. This is likely because of the enhanced habitat heterogeneity inside the shrub patches, with a more diverse plant community, and a wider range of niches. Also, the shrubs in the vegetation islands provide lower temperature and higher soil humidity. These results agree with those of Athias (1976), who concluded that the temperature, soil humidity and the amount of litter of the herbaceous plants were important for the invertebrate composition in burnt savannas in the Ivory Coast. In Zaire (Africa), the communities of Oribatida species are organized along a successional gradient, starting from the dense forest (''muhulu'') passing through woodland (''miombo'') to the savanna, providing evidence that the vegetation structure had a strong influence on animals through modification of microclimate (Noti et al., 1996). Pozo (1986) found similar patterns for collembolan populations. However, in savanna at High Katanga (Congo, Africa) there was no major difference between the oribatid mites fauna taken at the base of grass-tuft or between them, as the soil is completely covered by a layer of litter that allows fauna exchanges between the two habitats (Noti et al., 2003), providing a ''corridor'' that probably has attenuated the negative effects of fragmentation (Rantalainen et al., 2004), that is not the case of the savannas areas in Alter do Chão.

4.4. The effect of shrub species on the invertebrate communities

The effect of the shrub species on the soil fauna was less evident. Analyzing the samples collected under shrubs together with those sampled under the grass-tuft, we detected only a probable effect (type II error) of the shrub specie on the non-mite, non-collembolan community. The same effect was detected for the non-mite, non-collembolan community sampled under shrubs.

In spite of evidence of close association between arthropods and plant species on poorer soils detected for blanket bog (Blackith, 1974) and steppe (Stebaeva, 1963), we did not detect a strong effect of the shrub species for the all-invertebrate community. In our study, the zoological groups and the non-mite and non-collembolan community demonstrated a probable qualitative difference in relation to this factor. Probably, we did not find influence of the shrub species on the total invertebrate community because this community is dominated by the great abundance of Oribatida and Collembola. Franco et al. (1979) in the northern Mojave desert (US) also found little if any effect of shrub species on the number of arthropods beneath them. Furthermore, they concluded that the shrubs are similar not only in average arthropod density but also in the manner in which arthropod density is affected by depth and distance from the plant.

However, there were probable differences caused by plant species identity on the less dominant taxa (non-mite, non-collembolan community). The higher densities can be masking the effects when they are included in the analysis. The Oribatida colonize a great variety of habitats, have a great diversity of feeding and reproductive strategies, complex and diverse life cycles, and great morphological diversity (Lebrun et al., 1995). Depending on what food resources are available, collembolans and Oribatida may feed on fungi, algae, amorphous detritus or even other soil animals, thereby functioning as microherbivores, herbivores, detritivores or even predators (Scheu, 2002).

4.5. Zoological groups of higher taxonomic ranks: are they sufficient to show the differences among soil invertebrates in an Amazonian savanna?

Aggregating the invertebrates to higher taxonomic levels (zoological groups), we detected effects of soil type, vegetation structure and plant species identity on the composition of the savanna mesofauna community. The results indicate that conservation of invertebrate community in the savanna areas of Alter do Chão will depend on the conservation of the vegetation structure and plant diversity. We consider that the level of taxonomic resolution of the invertebrates utilized in our study was sufficient only to show the main differences of the spatial variation in community structure.

Soil macrofauna classified at higher taxonomic level (class, order and family; 27 faunal community variables) also showed effects of land-use in western Brazilian Amazonia (Barros et al., 2002), as the principal components analysis clearly separated pasture from disturbed forest, fallow, annual crop, and agroforestry system. In marine soft-bottom communities, Olsgard et al. (2003) showed that species richness was strongly correlated with species richness of genera, families and orders, which indicates that even after aggregation of data to higher taxonomic levels, the richness of the sites within the various investigated areas is retained. A study comparing three approaches to TS (morphoespecies, genera and seven functional groups) in ground ants in an eucalypt plantation, woodland regrowth patches and the surrounding grassland in Australia, revealed that: (1) morphoespecies and genus richness was highly correlated with species richness; (2) ordination scatterplots using species, morphoespecies and genus data revealed similar patterns of site separation; (3) functional group ordination separated all three habitats types for untransformed data (Pik et al., 1999). Resources spared by using TS could be allocated toward more frequent sampling events rather than identification of ant species (Schnell et al., 2003).

We must consider that TS for detecting habitat-related changes in invertebrate communities in Amazonia is unknown as most studies have used classification at the level of class, order or family. In some cases, TS represent a valid tool in routine monitoring but poorly known systems or baseline biodiversity and TS are simply incompatible, and it is only acceptable to detect impacts (Terlizzi et al., 2003). Among the soil invertebrates there is a considerable variability in the interactions of the different communities with their biotic and abiotic

environment, principally in a complex region like Amazonia. Communities are not well-integrated units that move in masse. They are collection of organisms and species that will respond individualistically to temporal variation, as they do to spatial variation (Levin, 1995). In this aspect, our analyses can be obscuring much more complex habitat partitioning occurring at the species level. Therefore, due to time and money constraints and a lack of taxonomic literature and expertise, mapping biodiversity of large geographical areas is impracticable and often impos-sible if the traditional measure of specie richness is to be used (Olsgard et al., 2003).

Appendix A

Density and number of zoological groups of soil invertebrates in savannas on clayey and sandy soils (mean of three values) in Amazonian-type savanna areas of Alter do Chão. Pará, Brazil. Standard errors in parentheses; S = shrub; G = grass-tuft.

Zoological groups	Savanna															
	Clayey soil								Sandy soil							
	M. sylvatica		M. albicans		M. caerulescens		C. ribesioides		M. sylvatica		M. albicans		M. caerulescens		C. ribesioides	
	S	G	S	G	S	G	S	G	S	G	S	G	S	G	S	G
Acari (Oribatida)	31.3 (10.2)	36.0 (26.6)	16.2 (6.7)	12.0 (7.6)	22.3 (6.1)	23.0 (10.5)	15.3 (6.9)	11.0 (5.0)	132.7 (40.8)	12.0 (7.8)	33.0 (17.5)	2.3 (0.3)	8.3 (6.4)	5.3 (3.4)	19.3 (9.4)	3.7 (2.0)
Acari Non-Oribatida	75.0 (27.2)	79.7 (71.7)	25.7 (15.6)	18.3 (12.3)	35.7 (19.7)	40.0 (13.5)	15.0 (4.0)	62.3 (27.4)	34.7 (2.2)	17.3 (2.0)	56.3 (42.0)	15.0 (7.6)	9.7 (4.7)	21.7 (12.0)	15.7 (2.3)	13.0 (6.9)
Araneae	0 (0)	0.7 (0.7)	0 (0)	0 (0)	0.7 (0.6)	0.3 (0.3)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)
Chilopoda	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)
Coleoptera (adults)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	3.0 (2.1)	0 (0)	1.0 (0.6)	0 (0)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0 (0)
Coleoptera (immatures)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0.7 (0.6)	0.7 (0.6)	0 (0)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)
Collembola	3.7 (1.8)	0.3 (0.3)	5.5 (3.0)	0 (0)	2.0 (1.1)	0.3 (0.3)	0.3 (0.3)	0 (0)	37.7 (10.9)	3.0 (1.5)	11.3 (7.3)	0 (0)	4.3 (2.3)	0.7 (0.6)	4.3 (2.2)	1.0 (0.6)
Diplura	0 (0)	0.3 (0.3)	1.0 (0.5)	0.7 (0.6)	2.0 (0.6)	0.7 (0.3)	1.3 (1.3)	0 (0)	3.7 (0.9)	0 (0)	1.0 (0.0)	0 (0)	1.0 (0.6)	0 (0)	1.7 (1.7)	0 (0)
Diptera (adults)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Diptera (immatures)	0 (0)	1.3 (0.9)	0 (0)	0 (0)	0.7 (0.6)	0.7 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Formicidae	0.3 (0.3)	0.3 (0.3)	3.2 (3.7)	0.7 (0.6)	0.7 (0.6)	0 (0)	0 (0)	1.0 (0.6)	11.0 (10.5)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0 (0)
Hemiptera (adults)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)
Homoptera (adults)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.7 (0.3)	0.7 (0.6)	0.3 (0.3)	0.3 (0.3)
Homoptera (immatures)	2.3 (0.9)	3.3 (2.4)	6.7 (7.0)	1.0 (0.9)	6.0 (1.7)	5.0 (4.0)	0 (0)	0.7 (0.6)	10.3 (5.2)	16.7 (14.3)	4.3 (3.4)	1.0 (0.6)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)
Hymenoptera (adults)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0.7 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Isopoda	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	1.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)	1.7 (1.7)	0 (0)	0 (0)	0 (0)
Isoptera	1.0 (0.9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.0 (0.9)	4.3 (2.9)	0.7 (0.3)	0 (0)	0.3 (0.3)	0 (0)
Lepidoptera (immatures)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Orthoptera	0 (0)	0 (0)	0.3	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0.3 (0.3)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Pauropoda	0 (0)	7.3 (7.3)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Phalangida	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.7 (0.6)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Protura	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	3.3 (1.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Pseudoscorpinida	1.0 (0.6)	0 (0)	0 (0)	0 (0)	1.0 (0.9)	0 (0)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Psocoptera	2.3 (1.4)	0.3 (0.3)	0.8 (0.3)	1.3 (0.6)	1.0 (0.0)	2.3 (2.3)	7 (0.3)	1.0 (0.9)	0 (0)	1.3 (0.6)	0.3 (0.3)	2.3 (0.3)	0.3 (0.3)	2.0 (1.1)	0.7 (0.6)	2.0 (1.2)
Symphyla	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Thysanoptera (adults)	2.0 (1.1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.0 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Thysanoptera (immatures)	0 (0)	0 (0)	0.3 (0.3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total	119.7 (19.6)	129.7 (106.3)	81.3 (15.8)	34.3 (10.7)	73.0 (24.0)	73.0 (9.0)	34.3 (12.6)	76.0 (31.6)	240.3 (69.1)	52.7 (5.2)	111.0 (40.0)	25.3 (7.5)	28.3 (8.8)	31.3 (12.7)	44.3 (14.6)	20.0 (9.1)
Number of zoological groups	11	10	10	7	14	10	11	5	14	10	15	6	13	8	12	5

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