

ORIBATID ASSEMBLIES OF TROPICAL HIGH MOUNTAINS ON SOME POINTS OF THE „GONDWANA-BRIDGE” – A CASE STUDY

(METHODOLOGICAL POSSIBILITIES OF COENOLOGICAL INDICATION
BASED ON ORIBATID MITES № 1.)

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Abstract. This work is the first part of a series of studies, which introduces the methodological possibilities of coenological and zoogeographical indication and – following the climate, vegetation and elevation zones – the pattern-describing analysis of the main Oribatid sinusia of the world explored till our days. This current work is a case-study, which displays the comparison of 9 examination sites from 3 different geographical locations. On each location, three vegetation types have been examined: a plain rain-forest, a mossforest and a mountainous paramo. Analyses are based on the hitherto non-published genus-level database and coenological tables of the deceased János Balogh professor. Occurrence of 18 genera is going to be published as new data for the given zoogeographical region.

Keywords: *Oribatid mites, rainforest, mossforest, paramo, Costa Rica, Brazil, Papua New-Guinea, similarity pattern, coenology, community, assembly*

Introduction

Oribatid mites of the tropical regions had been almost completely unknown for science before 1958. With the general use of the Berlese-funnel, systematic collections started at that time, which resulted in the collection of hundreds or thousands of species. However, the majority of these samples are unprocessed till these days. Professor J. Balogh and his fellow-workers had to realize, that the description of all the species living there is an impossible task.

And even if the recognizable morphological kinds of the samples will be described with decades of monumental work by the practices of formal describing taxonomy and according to the rules of nomenclature, the biological and coenological information content of these would still remain hidden. However the material extracted with the Berlese-Tullgren device informs us not only about the presence and morphological diversity, but also about the species' abundance and dominance as well. Moreover it has

become clear that this material together, as it was brought in front of us, contains a heap of such kind of information, which would be impossible to read from single species or from their constitutional characteristics. The samples collected this way are suitable for zoocenological examinations. This observation led Humboldt to the recognition of „basic forms” (Grundformen) and later to the revelation of formations, which means the structure that can be found in plant associations without the exact knowledge of species. The emphasis here is on the „visibility” of the vegetation, because the recognition of biological communities began with the sight of the flora: vegetation is a „landscape element”. Animal communities – apart from some exceptions – live hidden in the vegetation. But the Berlese-device concentrates and makes them visible.

Supported by the Division of Natural Sciences of UNESCO, and then with the help from other sources and by decades-long, even currently running work, J. Balogh and his followers (the senior authors of this paper among them) have been taking surveying collections in the tropical rainforest soils of Africa, South-America, South-East-Asia, New Guinea and of the islands of the world’s oceans. The picture drawn by the experiences gathered on three continents shows a disastrous destruction of natural vegetation, first of all tropical rainforests. If soil zoology wants to keep pace with this devastation, such a new, global research plan has to be made which provides before long a globally perspicuous picture of Oribatid fauna. Obviously, traditional museological and phenetic taxonomical methods in themselves are unsuitable for this task. In the view of collection technique, Berlese-device provides a unique advantage. Based on the available results of explorative field work the time has come to explore the hidden zoocenological information in the structure of Oribatid-associations and thus pave the way towards the forming of exact, academic hypotheses.

It would have been impossible to survey the whole tropical zone of the Earth. This is why two broad, representative belts have been chosen. The first of them follows the range of Andes, spreads from the Tropic of Cancer to the Tropic of Capricorn and not only covers the range of Andes, but also the broad tropical belt lying to the East of them. The 6000 m high ridge of Andes forces the clouds arriving from the direction of the ocean to ascend. Thus, on the Eastern slope of the mountain, zonation of luxuriant mountain forest and mossforest can be found. It has been planned that collections between the two Tropics, at different latitudes would be made through the Andes in zonal transects, and also in a regional transect which crosses the whole continent. The tropical zone of South America contains a mountain which is independent from the range of Andes: the Serra do Mar, and there’s also a parallel range of Serra do Mantiguéra which lies to the Northeast of Sao Paulo on the coast of the Atlantic Ocean. It lies on the most densely populated area of Brazil; therefore 95 % of its vegetation has already been destroyed. Recently, authorities try their hardest to save what is possible for science. This is the reason why the Hungarian research group also involved this region into their examinations. Their collection spots were located in 5 broad transect belts of the Neotropical Region. The first belt follows by and large the 20., the second the 10. grade of Northern latitude, the third the Equator, the fourth and fifth the 10. and 20. grade of Southern latitude (see sketch-map).

The other representative belt begins at the tropical coasts of Australia by Rockhampton, crosses Great Dividing Range and breaks 5 degrees to the South of Equator in Papua New-Guinea, at Owen Stanley Range. No other greater mainland can be found to the north of the Equator in this belt. Collections have been made at two

important areas to the East of the Australia-New Guinea line: in New Caledonia (north from the Tropic of Capricorn) and in the Hawaii-islands (south from the Tropic of Cancer). As it is known, the subduction of Australian Plate is to the east from New Caledonia, in the „Hebride-ditch“. These two area belts are connected with their common Gondwana-past. Plates which lie on the present area of South-America represent the Western, and those of New-Caledonia and New-Guinea represent the Eastern territories of Gondwanaland.

These two area-belts which were selected for examination are not only connected by their common Gondwana-past, but also by the spread of two plant genera: *Araucaria* and *Nothofagus*. Both connect Neotropical Region with Notogaea in the shape of a giant „U“. The South-American branch of this „U-shape“ follows by and large the range of Andes, but it is split into two parts around the Tropic of Capricorn and forms the Serra do Mantiguera- Serra do Mar twin mountain ranges in South Brazil. The two branches of the giant U-shape meet at Antarctica. The continuity is testified here partly by fossil remnants and partly by *Araucaria* and *Nothofagus* fossil pollen. The Eastern branch of the U-shape lies on the New-Zealand- New Caledonia – New-Guinea line and ends below the Equator. *Araucaria* formed great forests in South-Brazil, Argentina and Chile, but most of them are destroyed by these days. However, even nowadays there are great stands in New-Guinea. The gene centre of *Araucaria* is in New-Caledonia, 13 of the known 19 species live here (Schmidt, 1981). The range of *Nothofagus* is roughly identical to *Araucaria*. Great populations can be found on the temperate parts of Argentina and Chile and in New-Zealand. Its gene centre is in New-Guinea, where significant part of the known species lives.

The areas selected for examination were further narrowed down by concentrating our collections mainly to the humid tropics. Most of our collection sites had been on locations where vegetation formed closed forests due to abundant precipitation. These areas were: zones of tropical rainforest, tropical mountain forest and tropical mossforest, and even grass areas above forest threshold.

Beside vegetation types, the composition of Oribatid species is decisively influenced also by macroclimatic conditions. The data of Walter and Lieth Climatic Atlas, the so-called climatic graphs provide sufficient information on the annual or even daily changes of the macroclimatic conditions of the examined sites. Walter and Lieth discloses such kind of data on more than 10,000 locations of the Earth. Data are disclosed by continents and inside the continents, by climatic zones. This way, direct or indirect, but adequate data can be found for any location of the Earth. The vegetation type and the applying climatic graph can provide such kind of particular information, that the generic composition of the Oribatid sinusium can be described with great probability – even if we collect Oribatids on the site for the first time.

The Berlese-samples had been recorded separately, according to vegetation levels (substrate types). Main substrates were: soil, litter, moss, hanging litter, bark, epiphytes, canopy; and various transitions or combinations of these. Oribatids which were collected in the identical level (substrate-type), identical locality and extracted with Berlese-Tullgren device have been considered as units of examination. This material has been called Oribatid-sinusium. In one level, generally 2-10 – and in some exceptional cases even more – parallel materials have been collected. These were extracted and examined separately, but the group of parallel materials collected from one locality has been considered as sinusium. The number of parallel samples of sinusia was intended to be chosen in such a way that it should represent the whole of the habitat

properly, so more prevalent substrates (and such, also sinusia) have been represented by more sample units. Between 1965 and 1995, there have been 20 collecting journeys altogether in those representative belts with the purpose of collecting Berlese-samples available for coenological analysis. The sinusia collected from different areas have been distributed as follows:

Neotropical Region

| | |
|------------|-----|
| Cuba | 80 |
| Costa Rica | 141 |
| Ecuador | 207 |
| Brazil | 386 |

Australia and Oceania

| | |
|--------------------|-----|
| Tropical Australia | 82 |
| New-Caledonia | 133 |
| New-Guinea | 394 |
| Hawaii Islands | 95 |

Later on, these were supplemented with further samples:

According to the climatic classification of Walter and Breckle (1983), the area of rainforest clusters around Sao Paulo and Rio de Janeiro belongs to the group of extraequatorial tropical rainforests. However, relatively far from the Equator, in the zone of seasonal rainfalls – Zonobiome II (ZB II) – due to the effect of abundant rainfalls coming from the direction of the Atlantic Ocean, a perhumid Subzoobiome (sZB II/e I) is formed on the shore. This is also called tropical rainforest for simplicity.

The daily fluctuation of the temperature in the typical equatorial rainforests – especially in the soil – is quite negligible, and the mean annual temperature hardly changes. The situation is similar in the perhumid Subzoobiome of Zonobiome II. In the Orobiomes - which join to the tropical Zonobiomes – or tropical mountains, the annual mean temperature changes by 0.5-0.6°C in average with every 100 m increase in elevation above sea level. The fluctuation in the temperature has a decisive influence on the fauna of tropical rainforest and also to their soil fauna. Species with small tolerance – the so-called stenotherm species – can survive only in flatland or low-mountain jungles. The upper limit of their prevalence is – depending on the geographical latitude of the area – about 1000 m elevation above sea level. The next vertical prevalence limit is around 1700-2000 m, where the tropical rainforest is replaced by tropical mossforest. The diversity of the soil fauna is the greatest in this region. Above the tree line, the fauna changes completely, diversity sharply decreases and species with extreme cold tolerance appear.

Objectives

In this present section of our examinations, we set the objective to clarify the methodological possibilities of biological indication and the information content of the coenological data matrices by an appropriately chosen indication case study. We also set the aim to apply univariate indicators and to exploit the possibilities of multivariate coenological pattern analysis.

In this study, we attempted to answer the following indicational questions (exploring the following phenomena):

Taxonomical questions and their indicators

1. Is the average species number of those genera where the present individuals belong to characteristic to a habitat or not? (Indicator: The arithmetic average, empirical variance and relative variance of the species number of Oribatid genera present in the examined habitat weighted by constancies).
2. Is the information on the extent of taxonomical isolation of present genera characteristic for a habitat? (Indicator: The average number of genera, its empirical variance and relative variance of the family number of Oribatid genera present in the examined habitat).

Zoogeographical questions and their indicators

3. Is the information on the worldwide spread of species belonging to the present genera characteristic for a habitat? (Indicator: presence in the examined habitats of the species belonging to the examined Oribatid genera in the main zoogeographical regions with the method of “simple voting”.)

Question of spatial heterogeneity and its indicator

4. Is the information on the extent of difference in the genus composition of the different soil samples collected from the same habitat characteristic for a habitat? (Indicator: the average pairwise dissimilarity of samples collected from the same habitat (with distance functions calculated for the presence of genera), as a coenological heterogeneity indicator).

Coenological (multivariate) questions and their indicators

5. Is the similarity pattern of genera of different habitats informative on the type and/or geographical location of the habitat? (Indicator: the multivariate similarity pattern of Oribatid community of habitats).
6. Is the similarity pattern of Oribatid genera in soil samples collected from different habitats informative on the type and/or geographical location of the habitat? (Indicator: the multivariate similarity pattern of Oribatid community of individual soil samples of habitats).
7. The type or the geographical location of a habitat plays bigger role in the formation of the present Oribatid fauna? (Indicator: linear regression model).

Review of literature

Berlese and Grandjean

The establishment of Oribatology in the last 100 years can be linked to two great persons: A. Berlese and F. Grandjean. If we look at the dates of the first and last publications of these two persons (Berlese: 1880-1923; Grandjean: 1928-1974), we can recognize the beginning and the end of two 50-year long eras. The first period, among many other things, provided us with an outstanding extraction method: the Berlese

device. This method – regarding its significance – can be compared to the invention of the microscope. It led us to the exploration of a new, unknown microcosm: the mezofauna of the soil and thus, the establishment of a new field of science: soil zoology. In the second era, a congenial scientist – F. Grandjean – not only spotted the most subtle structures under his microscope, but also unravelled the principles of hundreds of millions years of evolution. It is not so self-explanatory that these two aspects do not exclude, but on the contrary, they supplement each other. If the subject of the branch of biological discipline is the existing, given living organism in its timeless existence (esse, being, das Sein), then we speak about the present, current branch of discipline. This is the aspect of Berlese's work of life. And if the subject of the biological discipline is the genesis, past, evolution of the living organism, in other words, its existence through the time (fieri, becoming, das Wesen), we speak about a genetic branch of discipline. This is the essence of Grandjean's work-life. To understand the structure and functioning of biosphere, we have to learn the components of the whole system in a form they exist today. Then we have to learn their evolutionary past, where they originate from. This is how the two aspects can be linked to each other. Problems arise with the fact that these two aspects work with different objectives. Those who study the Oribatid fauna of the world, the Oribatid assemblies in the ecosystems, want to give little but important information on as many species as possible, because such kind of differentiating characteristics are sufficient for the recognition of the building elements of these assemblies. And those, who deal with the evolution of Oribatids, want to obtain a tremendous number of data - which are important from the aspect of evolution - but only on a little number of species. Since the Hungarian research team dealt with the examination of Oribatid assemblies and their spatial distribution of Oribatids, they represent the first group of oribatologists.

Further international studies

The „first wave” of research started in 1958. By that time we have to differentiate between preliminary and general collections. On the first place we mention the exemplary work of Aoki et al. in Japan and Eastern Asia. The subantarctic research of Wallwork is of general significance, however his work in Ghana and his further African works can be considered only as preliminary studies. In the „second wave” which started in the late sixties, - among many others - the works of Engelbrecht (1969) and his fellow researchers in South Africa; Corpus-Raros (1979) on the Philippines, Lee (1980) in Australia, Pérez-Inigo and Baggio (1980) in Brazil, Bhattacharia et al. (1972) and Haq (1980) can be considered to be of general importance.

Hammer and Beck

The fact that 90 % of tropical Oribatid species were unknown until the late fifties, made coenological examinations impossible, however there have been many attempts to reach this goal. Hammer (1958-1962) published four fundamental works on the Oribatids of the South American Andes, partly even from tropical areas. Starting from Peru, down to the Tierra del Fuego he collected almost 50,000 Oribatid specimens. He identified the whole collection and found 466 species, of which 324 were unknown. Thus he laid down the basics of the description of the South-American Oribatid fauna. He also started the coenological processing of the material, but the taxonomic work exhausted him in such an extent that he hadn't had the time to complete this work. The

fundamental work of Beck (1963) has a similar significance. He examined mites in only one region of Peru, in the main vegetation zones of the Andes. He completed 300 Berlese-collections with more than 350,000 specimens. A significant part of the examined material belonged to the Oribatids. He made important statements primarily concerning the „autoecology“ of the species, but the huge number of undescribed species made coenological analysis impossible. The holistic point of view is characteristic both to Hammer and Beck. They applied their examinations not only to individual species but to the whole Oribatid community. Unfortunately, there has been a fundamental difference between the point of view of Hammer and Beck. Hammer was driven primarily by biogeographical problems; he wanted to learn the regional distribution of Oribatids. This is why he marked his collection spots in a range of thousands of kilometers from Peru to the Tierra del Fuego (Land of Fire). Beck based his studies on the different elevation zones of vegetation, so he studied the zonal distribution of species. It is obvious, that a world-wide study requires both of them, and the Hungarian research team planned an examination exactly of this kind. In their plan, both regionality and zonality obtained their roles.

General findings of the coenological Oribatid examinations

The greatest experience of a first look on an extracted Berlese-material is that unevenness can be found in the Oribatid assemblies. Some species appear in great numbers, while only a few can be seen from others. The second experience has been that if we repeat the collection over and over again, certain species appear constantly. Species with great numbers are called dominant, and the ever-appearing are called constant species. These two characteristics can be experienced often by the same species, so these are called constant-dominant species. According to the third experience, there are some species, which live only in certain kinds of Oribatid assemblies; they can be collected only in that combination of species. These are called character species. And according to the fourth experience, certain Oribatid species – however, apparently there’s no direct connection among them – always appear together in the Oribatid assemblies.

New results of Oribatid bioindicational studies

Analysing the suitability of Oribatids for indication purposes, many authors point out their long life-span, slow growth and slow dispersion ability. Based upon these characteristics, Oribatids can be used as strong indicators of their environment (Gulvik 2007). Current bioindicational studies based on Oribatids use just the measures of Oribatid abundance or species richness at most. A significant part of these studies are directed to analyse anthropogenic effects. According to Niedbala (1990), every kind of human interference decreases the abundance and species richness of the mites. Oribatids are thought suitable – though in different extent – for bioindication purposes in respect of chemical pollutions according to works of Andres 1999, Braman 1993, Liiri 2002, Miglorini 2005, Prinzing 2002, Zaitsev 2001, Seniczak 1995, Skubala 2004, Stamou 1995, Steiner 1995, Straalen 2001 and Osler 2006. Many authors refer to the role of moisture and organic material content of the soil in affecting the abundance of Oribatids (Braman 1993, Siepel 1996, O’Lear 1999, Kovac 2001, Tsiafouli 2005, Altersor 2006); however their statements concerning the direction of these effects are contradictory. This is not surprising, since different communities had been examined. Based on

surveys of different approaches, effects of human indicated changes in the structure of vegetation (grazing, agricultural cultivation, forestry etc.) seem to be clear (Migliorini 2003, Lindo 2004, Altesor 2006, Berch 2007, Cole 2008), since disturbances of vegetation result in lower Oribatid abundance. We think however that the role of anthropogenic effects can only be entirely understood if the reasons and patterns of naturally induced variability in community structure were explored first, since these can be considered a reliable reference in the evaluation of anthropogenic disturbances. Examining the effects of different vegetation types and floral succession stages, many authors (Noti 1996, Salmon 2006, Osler 2001 és 2006, Coleman 2008) describe high Oribatid abundance and species richness in natural or almost natural habitat types. These authors also point out that the role of definite plant species, substrate types and microhabitats does not seem to be significant from the aspect of the composition of Oribatid communities (Kaneko 2005, Franklin 2005, Fagan 2006, Lindo 2006), though contradictory data also exist (Coulson 2003). By analyzing African Oribatid communities, Noti (2003) attributed the most significant effect to vegetation type, followed by moisture content, then organic material content, C/N ratio and N-content in respect of species richness.

Materials and methods

Examined areas and their vegetation

This work is intended to be the first part of a series of studies consisting of several parts. In this study series, we want to introduce the main Oribatid sinusia of tropical areas as per climatic, vegetation and elevation zones. According to the holistic approach, we start from the whole and proceed towards the smaller parts. As a first step, we examined the similarities between the Oribatid sinusia of the Neotropical Region and the Notogaea. Stemming from the fact that the vertical stratification of Oribatid fauna follows the vegetation zones, we took samples for examination from 3 elevation zones:

1. tropical rainforest
2. mossforest
3. paramo

In the study, we disregarded the mountain forest zone, which can be found between the zones of tropical rainforest and mossforest, because the determination of its borders is quite uncertain. To avoid transitions, Berlese-samples of tropical rainforest have been selected from 200 m elevation above sea level, close to the forest border. 2 ideal transects were set for representative sampling. The first one crosses Andes at Costa Rica, at the 10. degree of latitude, from coast to coast. The second one starts from Papua New-Guinea, from the valley of Fly River at the 4. degree of Southern latitude, and goes up to the 4000 m high ridge of Mt Wilhelm. As an amendment, samples were also taken near to the 23. degree of Southern latitude in an additional transect, crossing Serra do Mar and Serra do Mantiguera. This transect has been set because 200-300 years ago there's been a belt of dense tropical rainforest – which even exceeded Amazonia in biodiversity – in the most densely populated area of Brazil, along the line marked by Sao Paulo and Rio de Janeiro. Almost 95 % of these forests have been devastated, but it could have been hoped that the rainforest spots reserved the original soil fauna – at least

partially. 82 representative samples have been collected on 9 spots of the three transects. The spatial distribution of these samples and the abbreviation of individual sites can be seen in the next table:

| | Tropical rainforest | Mossforest | Paramo | |
|------------|------------------------|------------|--------|----|
| Costa Rica | RC: 10 | MC: 10 | PC: 10 | 30 |
| Brazil | RB: 7 | MB: 6 | PB: 10 | 23 |
| New-Guinea | RN: 10 | MN: 9 | PN: 10 | 29 |
| | 27 | 25 | 30 | 82 |

Taxonomical processing of the collected material

Oribatid mites are one of the land animals with the highest population density. Their abundance among tropical conditions can exceed one million individuals per square meter, but even among the conditions of the temperate zone, their density is 50,000-500,000 per square meter, while in agricultural areas this measure is around 25,000 in average (Coleman et al. 2004). Their numbers are also significant in treebark (Erdman 2006) and foliage (Winchester 1997, Behan-Pelletier and Walter, 2000). Using 16, 32 or more Berlese-devices during many years in a worldwide sample collection we get such an extreme amount of individuals, which is impossible to identify completely. Given such a worldwide programme, set forth by the Hungarian research group, the processing of the entire material is even more inconceivable. Thus we decided to render the second level of the system, the genus, as the base of the processing. Members of our research group – formerly led by János Balogh – knew well before the initiation of coenological analysis that the genus could be the taxonomical level which can bear valuable information for an examination of such a magnitude. Using species as a category at the current level of Oribatid taxonomy would be an entirely hollow task, since the decisive majority of the described morphological species apparently have no valuable ecological or evolutionary information content. Thus, it is not a coincidence that the work of Hammer and Wallwork (1979) on the connection between the worldwide distribution and continental migration of Oribatids is based on generic distribution from the beginning to the end. Most biogeographical and many ecological studies do so in connection with other groups of animals. This is not a coincidence, but a consequence originating from the past and (unfortunately) the current practice of species description. The interpretation of species of the phenetic descriptive taxonomy is under the subjective approach of the describing taxonomist, since there are no uniform rules in this respect. If an individual is found to be different from the formerly described species in 2-3 seemingly independent morphological characteristics, then it is usually automatically considered as a new taxon. Descriptive taxonomists are interested in the propagation of the number of nominal species, and in accordance with the aforementioned, their activity is not subjected to strict scientific critics. Thus the question whether a species described correctly from the aspect of nomenclature can be considered as a new inherent biological entity or not, usually does not even emerge. Resulting from quite understandable reasons, the modus operandi is eclectic even by the description of these nominal species. Conspicuous, easily identifiable species have been preferred. In large genera with many species, much less species is described because it requires more work and unproductive intellectual efforts. Early auctors strove to briefness, listing of the differentiating characteristics by the description of species, thus

the more general characteristics; really important biological strains were put forward during the description of genera. As a consequence, it is quite possible that slightly different species from the same genus represent only the variability within the biological species. Obviously, to unveil this, is an important scientific task.

The generic exploration of the Oribatid mites of the world among the current conditions seems to be sufficient from the aspect of the valuable biological research, and the genera tend to represent real biological phenomena more likely than the infinite nominal species.

Despite these grave scientific problems, coenological, zoogeographical and ecological studies are compelled to use the classic morphological, descriptive taxonomical works as a base until molecular techniques capable of the definite identification of kinds do not become simple, fast and cheap enough for the routine processing of large materials.

Assembling coenological tables

The base table for our analyses was the 82 individual soil samples from the 9 examined habitat (3 habitat types of 3 areas) containing 111 Oribatid genera. For the various analyses, we created task-oriented assemblies from this base table. We created the constancy table of the genera of the 9 habitats, where the constancy values of the individual genera have been estimated by the relative occurrences in the related samples (*Table 1*). As a complementary data source, we created the occurrence table of the same genera in the zoogeographical regions based on the monography of Balogh and Balogh 1992, complemented with own, new data (*Table 2*). Using the same monography as a reference, we looked up the number of species of the genera, and the number of genera of the families which we used as complementary information for the analyses. Based on all of the individual samples, paired all samples with all other samples we created the similarity matrix of our data using multiple distance functions. In this current publication, Euclidean distance, PHI coefficient and Jaccard function have been used.

Methods for analyzing coenological tables

We created the indicators marked by our objectives from our coenological tables, and analysed the values of these indicators in the different sites. As a taxonomical indicator, we calculated the average number of species of genera found in individual habitats weighted by the constancies (and also its empirical and relative variance), and the average number of families of the same genera (and variances). As a zoogeographical indicator, we introduced the method of “simple voting”, where the occurring genera give one vote for those geographic regions, where at least one of their representatives can be found. Occurrence of one genus in one region means 1 vote for the region in question. Votes of genera of a certain site given for different regions are represented as a % proportion of the total votes of these genera, what is characteristic for the habitat. We examined the constancies of genera on individual habitats, and the generic heterogeneity of the samples. The measure of heterogeneity was calculated by pairing every sample with all the other samples within a site. Based on the presence-absence data of their genera, we created their distance matrices and calculated the average of the distance values. After the evaluation of univariate indicators we analysed the similarity patterns of the sites with Non-Metric Multi-Dimensional Scaling (NMDS) and Hierarchical Cluster Analysis (HC-UPGMA) using multiple distance functions, then

we conducted these analyses on the tables of individual elementary samples. We applied multivariate regression modelling in order to further evaluate the results of multidimensional pattern analysis and to test our hypotheses. Gathered results have been evaluated collectively and compared with literature findings, then the examined habitat has been characterized by these results.

Results

Results of taxonomical processing of field samples

By the taxonomical processing of field samples we determined the occurrence data of the found genera, which have been made comparable by representing them in constancy %. Results are summarized in *Table 1*, where we marked the dominant genera (with mass occurrence) by underlining beside the constancy data. High constancy value and underlining together marks constant-dominant genera. Most rigorously constant-dominant genera are the **Xenillus** and the **Plasmobates** in the Brazilian mossforest, the **Oppia** in the New-Guinean mossforest, the **Allonothrus** in the Costa-Rican rainforest and the **Rostrozetes** in both the Costa-Rican and New-Guinean rainforests. According to our data, the **Eremulus**, **Eohypochthonius** and **Teleioliodes** genera are characteristic for the rainforests, the **Oppia** genus for the mossforests, and the **Scheloribates** genus for the paramos. Geographic characteristics can only be observed by the **Anderemaeus** genus for Brazil and the **Dolicheremaeus** genus for New-Guinea. We couldn't find a single genus characteristic for the American continent. **Malaconothrus** and **Microtegeus** genera could be found on all sites (general prevalence). Based on the monography of Balogh and Balogh 1992, occurrences of genera found by us in the zoogeographical regions of the world are summarized in *Table 2*. According to our own data, in comparison with the aforementioned monography, occurrence for the relating zoographical region of 18 genera can be published as new data, these are marked underlined. Based on the data of the table it is clearly visible that the **Malaconothrus** and **Microtegeus** genera (observed by us on all sites) are truly cosmopolites, similarly to the **Dolicheremaeus** genus, which we found characteristic to New-Guinea. However, the **Anderemaeus** is known only in Notogaea and the Neotropis. The **Scheloribates**, **Eremulus**, **Eohypochthonius**, **Rostrozetes**, **Plasmobates** and the **Oppia** genera are cosmopolites. The **Teleioliodes** genus can be considered prevalent in Gondwana. The **Xenillus** is known from Holarctis, Notogaea and Neotropis, and the **Allonothrus** genus is circumtropical. These data point out, that members of genera with very wide prevalence from purely geographical aspect are quite discriminative in respect of habitats, and thus can be informative for us.

Table 1. Constancy % of Oribatid genera found on individual sites

| GENUS | MB | MC | MN | PB | PC | PN | RB | RC | RN |
|--|-------|-------|-------|-------|-------|-------|-------|--------|-------|
| Achipteria | | 26.67 | | | | | | | |
| Acutozetes | | | | | | | | | 20.00 |
| Aeroppia | | | | | | | | 23.08 | |
| Afronothrus | | | | | | | | 38.46 | 13.33 |
| Allonothrus | | | | | | | | 100.00 | |
| Allozetes | | | | | | | | 7.69 | 13.33 |
| Anachipteria | | | | | 31.82 | | | | |
| Anderemaeus | 83.33 | | | 10.53 | | | 28.57 | | |
| Aokiella | | | | | | | | | 6.67 |
| Arceremaeus | | | | | | | | 30.77 | |
| Archegozetes | | | | | | | | 30.77 | 6.67 |
| Basilobelba | | | | | | | | 7.69 | |
| Bornemiszaella | | | | | | | | 23.08 | |
| Brazilozetes | | | | | | | 14.29 | | |
| Camisia | | | | 31.58 | 4.55 | | | | |
| Carabodes | | 46.67 | | | | | | 23.08 | |
| Caudameolus | | | | | | | 28.57 | | |
| Cavernocephus | | | | | | | | 7.69 | |
| Cepheus | | 13.33 | | | 40.91 | | | 15.38 | 13.33 |
| Ceratokalumma? =Achipterina | 66.67 | | | | | | | | |
| Ceratoppia | | | | | 4.55 | | | | |
| Ceratorchestes | 33.33 | 33.33 | | | 11.11 | | 28.57 | 38.46 | |
| Ceratozetes | | | | | 13.64 | | | | |
| Charassobates | 33.33 | | | | | | 28.57 | 15.38 | |
| Compactozetes | | | 33.33 | | | | | | |
| Crotonia | 66.67 | 80.00 | | 15.79 | 47.62 | | | | |
| Cubabodes | | | | | 25.00 | | | 7.69 | |
| Cultroribula | | | | | | 4.35 | | | |
| Cyrthermannia | | | | | | | | 30.77 | 73.33 |
| Dampfiella | | 26.67 | | | 27.27 | | 28.57 | 7.69 | 13.33 |
| Dendrohermannia | | | | | | | | | 40.00 |
| Dolicheremaeus | | | 33.33 | | | 21.74 | | | 80.00 |
| Edwardozetes | | | | 5.26 | 11.11 | 26.09 | | | |
| Eohypochthonius | | | | | | | 71.43 | 38.46 | 33.33 |
| Epilohmannia | | | | 5.26 | | | 71.43 | 53.85 | 6.67 |
| Eremaezetes | 16.67 | | | 10.53 | | | 28.57 | 61.54 | 66.67 |
| Eremobelba | 66.67 | | | 21.05 | | | 57.14 | 15.38 | 86.67 |
| Eremulus | | | | | | | 57.14 | 23.08 | 86.67 |
| Eupterotegaeus | 50.00 | 86.67 | | | 63.64 | | | | |
| Eutegaeus | 33.33 | | | 5.26 | | | | | |
| Furcobates | | 20 | | | 13.64 | | | | |
| Fuscozetes | | | | 5.26 | 50.00 | | | | |
| Galumna | | | | | | 4.35 | | | |
| Galumnella | | | | | | | | | 6.67 |
| Gressittolus | | | | | | | | | 13.33 |
| Gustavia | | | | | 22.22 | | | | |

| GENUS | MB | MC | MN | PB | PC | PN | RB | RC | RN |
|-------------------------|--------|-------|--------|-------|-------|-------|-------|--------|--------|
| Hammerabates | | | | | | 34.78 | | | |
| Hamotegaeus | | | | | 4.55 | | 28.57 | | |
| Haplozetes | | | | | | | | 7.69 | |
| Hardybodes | | | | | | | | | 26.67 |
| Hermannia | 33.33 | | | 5.26 | | | 57.14 | | 80.00 |
| Hermanniaella | 16.67 | 86.67 | | | 59.09 | | 71.43 | 30.77 | 20.00 |
| Heterobelba | 66.67 | 13.33 | | 5.26 | 12.50 | | 85.71 | 7.69 | |
| Heterozetes | | | 11.11 | | | | | | |
| Idiozetes | | | | | | | | | 20.00 |
| Indoribates | | | | | | | | | 6.67 |
| Lamellobates | | | | | | | 42.86 | 7.69 | |
| Liacarus | | 46.67 | | | | | | | |
| Licneremaeus | | | | | | | | 15.38 | |
| Limnozetes | | | | 5.26 | | | | | |
| Malacoangelia | | | | | | | | 16.67 | 60.00 |
| Malaconothrus | 50.00 | 60 | 22.22 | 42.11 | 31.82 | 21.74 | 71.43 | 92.31 | 73.33 |
| Masthermannia | | | | | | | | 15.38 | 53.33 |
| Microtegeus | 83.33 | 33.33 | 22.22 | 26.32 | 11.11 | 13.04 | 71.43 | 53.85 | 40.00 |
| Microzetes | | | | 21.05 | | | | | |
| Mochlozetes | | | | 42.86 | | | | 30.77 | |
| Mycobates | | | | 5.26 | 4.55 | | | | |
| Nanhermannia | 83.33 | 60 | | 63.16 | 50.00 | | 71.43 | | 28.57 |
| Neoribates | | | | | | | | | 53.33 |
| Nixozetes | | | | | | | | | 33.33 |
| Nodocephus | 50.00 | 26.67 | | 15.79 | 11.11 | | | 7.69 | |
| Nothrus | 16.67 | 46.67 | | 15.79 | 28.57 | | | | |
| Oppia | 83.33 | 93.33 | 100.00 | | | | | | |
| Oribatella | 66.67 | 26.67 | | | | | | 30.77 | 33.33 |
| Oribatula | | | | 57.89 | | | | | |
| Otocephus | | | | | | | | | 6.67 |
| Oxymerus | | | | | | | | | 40.00 |
| Pelops | | | 33.33 | | 31.82 | 4.35 | | 15.38 | |
| Peloribates | 66.67 | | | 47.37 | | | 42.86 | 7.69 | 46.67 |
| Phauloppia | | | | 5.26 | | | | | |
| Pheroliodes | 50.00 | | 11.11 | 21.05 | 16.67 | 21.74 | 71.43 | 7.69 | |
| Plasmobates | 100.00 | 60.00 | | 26.32 | 52.38 | | 71.43 | 30.77 | 66.67 |
| Plateremaeus | | | | | | | | 7.69 | 33.33 |
| Platynothrus | | 53.33 | 66.67 | 5.26 | 36.36 | 21.74 | | | |
| Protoribates | | | | | 27.27 | 4.35 | 28.57 | 15.38 | |
| Pseudotocephus | | | | | | | | 23.08 | |
| Pteroripoda | | 80.00 | | | | | | | |
| Reductobates | | | 11.11 | | | 17.39 | | | |
| Rhynchoppia | | | | | 23.08 | | | | |
| Rhynchoribates | 50.00 | 20.00 | | | | | 28.57 | 23.08 | |
| Rioppia | 16.67 | | | | | | 14.29 | 15.38 | |
| Rostrozetes | 100.00 | 60.00 | | 26.32 | 54.55 | | 71.43 | 100.00 | 100.00 |
| Scapheremaeus | | 80.00 | | 36.84 | 36.36 | 8.70 | | | |
| Scheloribates | | | | 73.6 | 72.73 | 26 | | | |
| Sphaerochthonius | | | | | | | | 7.69 | |
| Sternoppia | | | | | | | | 7.69 | |

| GENUS | MB | MC | MN | PB | PC | PN | RB | RC | RN |
|-----------------------|--------|-------|----|-------|-------|------|-------|-------|-------|
| Suctoribates | 83.33 | | | 5.26 | | | | | 13.33 |
| Tectocephus | 33.33 | 26.67 | | 5.26 | 45.45 | 8.70 | | | |
| Tegeocranellus | 66.67 | | | | | | 57.14 | | |
| Tegoribates | | | | 5.26 | 36.36 | | | | |
| Telelioides | | | | | | | 71.43 | 38.46 | 40.00 |
| Tentaculozetes | | | | | | | | | 20.00 |
| Trichoribates | | | | | 4.55 | | | | |
| Truncozetes | | | | | | | | 76.92 | |
| Tuberemaeus | | | | | | 4.35 | | | 60.00 |
| Williamszetes | | | | 21.05 | | | | | |
| Xenillus | 100.00 | | | 10.53 | 27.27 | | 85.71 | 15.38 | |
| Xiphobelba | | | | | | | | | 80.00 |
| Xylobates | | | | | | 8.70 | | | 93.33 |
| Zetorchestes | | | | | | | | | 26.67 |
| Zygoribatula | 16.67 | | | | 4.55 | 4.35 | | | |

Table 2. Number of species and presence characteristics of the examined genera according to Balogh and Balogh (1992). In the collected samples 18 genera were new to the fauna of the given zoogeographical region compared to this monography (bold underlined).

| GENUS / (Family) | ET | NO | HO | OR | AN | NE | Species number |
|--|----|----------|----|----|----|----------|----------------|
| Achipteria | 1 | | 1 | 1 | | <u>1</u> | 47 |
| Acutozetes | | 1 | | 1 | | | 5 |
| Aeroppia | | | | | | 1 | 11 |
| Afronthrus | 1 | 1 | | 1 | | 1 | 5 |
| Allonothrus | 1 | 1 | | 1 | | 1 | 12 |
| Allozetes | 1 | 1 | 1 | 1 | | <u>1</u> | 8 |
| Anachipteria | 1 | | 1 | | | <u>1</u> | 19 |
| Anderemaeus | | 1 | | | | 1 | 8 |
| Aokiella | | <u>1</u> | | 1 | | | 2 |
| Arceremaeus | | | | | | 1 | 4 |
| Archeozetes | | 1 | | 1 | | 1 | 5 |
| Basilobelba | 1 | 1 | | 1 | | 1 | 13 |
| Bornemiszaella | | | | | | 1 | 3 |
| Brazilozetes | | | | | | 1 | 3 |
| Camisia | 1 | 1 | 1 | 1 | 1 | 1 | 39 |
| Carabodes | 1 | 1 | 1 | 1 | | 1 | 130 |
| Caudameolus | | | | | | 1 | 1 |
| Cavernocephus | | | | | | 1 | 2 |
| Cepheus | 1 | <u>1</u> | 1 | | | 1 | 60 |
| Ceratokalumma? =Achipterina | 1 | 1 | | | | <u>1</u> | 4 |
| Ceratoppia | 1 | | 1 | 1 | | 1 | 17 |
| Ceratorchestes | | | | | | 1 | 4 |

| GENUS / (Family) | ET | NO | HO | OR | AN | NE | Species number |
|------------------------|----|----------|----|----|----|----------|----------------|
| Ceratozetes | 1 | 1 | 1 | 1 | 1 | 1 | 89 |
| Charassobates | | | | | | 1 | 7 |
| Compactozetes | | 1 | | | | | 4 |
| Crotonia | 1 | 1 | | | | 1 | 2 |
| Cubabodes | | | | | | 1 | 5 |
| Cultroribula | 1 | 1 | 1 | 1 | | 1 | 34 |
| Cyrthermannia | 1 | 1 | 1 | 1 | | 1 | 12 |
| Dampfiella | | 1 | | 1 | | 1 | 14 |
| Dendrohermannia | | 1 | | | | | 1 |
| Dolicheremaeus | 1 | 1 | 1 | 1 | 1 | 1 | 105 |
| Edwardozetes | | 1 | 1 | | 1 | 1 | 8 |
| Eohypochthonius | 1 | 1 | 1 | 1 | 1 | 1 | 6 |
| Epilohmannia | 1 | 1 | 1 | 1 | | 1 | 44 |
| Eremaezetes | 1 | 1 | | 1 | | 1 | 17 |
| Eremobelba | 1 | 1 | 1 | 1 | 1 | 1 | 38 |
| Eremulus | 1 | 1 | 1 | 1 | 1 | 1 | 27 |
| Eupterotegaeus | | | 1 | | | 1 | 9 |
| Eutegaeus | | 1 | | | | 1 | 11 |
| Furcobates | | | | | | 1 | 1 |
| Fuscozetes | | | 1 | | | <u>1</u> | 10 |
| Galumna | 1 | 1 | 1 | 1 | 1 | 1 | 207 |
| Galumnella | 1 | 1 | 1 | 1 | | 1 | 14 |
| Gressittolus | | 1 | | | | | 2 |
| Gustavia | 1 | <u>1</u> | 1 | 1 | | <u>1</u> | 18 |
| Hammerabates | 1 | 1 | | 1 | | | 4 |
| Hamotegaeus | | | | | | 1 | 4 |
| Haplozetes | 1 | 1 | 1 | 1 | | 1 | 11 |
| Hardybodes | | 1 | | | | | 1 |
| Hermannia | 1 | <u>1</u> | 1 | 1 | | <u>1</u> | 51 |
| Hermanniella | 1 | 1 | 1 | 1 | | <u>1</u> | 32 |
| Heterobelba | 1 | | | 1 | | 1 | 13 |
| Heterozetes | | <u>1</u> | 1 | 1 | | | 6 |
| Idiozetes | | <u>1</u> | | 1 | | | 2 |
| Indoribates | | <u>1</u> | | 1 | | | 2 |
| Lamellobates | 1 | 1 | 1 | 1 | | 1 | 11 |
| Liacarus | 1 | 1 | 1 | 1 | 1 | 1 | 80 |
| Licneremaeus | 1 | 1 | 1 | 1 | 1 | 1 | 18 |
| Limnozetes | | | 1 | 1 | | 1 | 17 |
| Malacoangelia | 1 | 1 | 1 | 1 | | 1 | 4 |
| Malaconothrus | 1 | 1 | 1 | 1 | 1 | 1 | 51 |
| Masthermannia | | 1 | 1 | 1 | | 1 | 5 |

| GENUS / (Family) | ET | NO | HO | OR | AN | NE | Species number |
|-------------------------|----|----------|----|----|----|----------|----------------|
| Microtegeus | 1 | 1 | 1 | 1 | | 1 | 22 |
| Microzetes | | | 1 | | | 1 | 13 |
| Mochlozetes | 1 | | 1 | | | 1 | 6 |
| Mycobates | | | 1 | | | 1 | 17 |
| Nanhermannia | 1 | 1 | 1 | 1 | | 1 | 29 |
| Neoribates | | 1 | 1 | | | | 19 |
| Nixozetes | | 1 | | 1 | | | 5 |
| Nodocephus | 1 | 1 | | | | 1 | 7 |
| Nothrus | 1 | 1 | 1 | 1 | 1 | 1 | 54 |
| Oppia | 1 | 1 | 1 | 1 | | 1 | 16 |
| Oribatella | 1 | 1 | 1 | 1 | | 1 | 113 |
| Oribatula | 1 | | 1 | 1 | | 1 | 80 |
| Otocephus | | <u>1</u> | | 1 | | 1 | 20 |
| Oxyamerus | | 1 | 1 | 1 | | | 6 |
| Pelops | 1 | 1 | 1 | 1 | 1 | 1 | 80 |
| Peloribates | 1 | 1 | 1 | 1 | 1 | 1 | 84 |
| Phauloppia | 1 | 1 | 1 | 1 | 1 | 1 | 27 |
| Pheroliodes | 1 | <u>1</u> | | | | 1 | 3 |
| Plasmobates | 1 | 1 | 1 | 1 | 1 | 1 | 19 |
| Plateremaeus | 1 | 1 | 1 | 1 | | 1 | 19 |
| Platynothrus | 1 | 1 | 1 | 1 | 1 | 1 | 31 |
| Protoribates | 1 | 1 | 1 | 1 | 1 | 1 | 50 |
| Pseudotocephus | 1 | 1 | | 1 | | 1 | 21 |
| Pteroripoda | | | | | | 1 | 1 |
| Reductobates | | 1 | | | | | 3 |
| Rhynchoppia | | 1 | | | | <u>1</u> | 1 |
| Rhynchoribates | 1 | | | 1 | | 1 | 22 |
| Rioppia | | | | | | 1 | 2 |
| Rostrozetes | 1 | 1 | 1 | 1 | 1 | 1 | 40 |
| Scapheremaeus | 1 | 1 | 1 | 1 | 1 | 1 | 50 |
| Scheloribates | 1 | 1 | 1 | 1 | 1 | 1 | 200 |
| Sphaerochthonius | 1 | 1 | 1 | 1 | 1 | 1 | 10 |
| Sternoppia | | | | | | 1 | 12 |
| Suctoribates | 1 | <u>1</u> | | 1 | | 1 | 3 |
| Tectocephus | 1 | 1 | 1 | 1 | | 1 | 37 |
| Tegeocranellus | 1 | 1 | 1 | 1 | | 1 | 8 |
| Tegoribates | 1 | | 1 | | | 1 | 9 |
| Teleioliodes | 1 | <u>1</u> | | | | 1 | 3 |
| Tentaculozetes | | 1 | | | | | 1 |
| Trichoribates | 1 | | 1 | | | 1 | 55 |
| Truncozetes | | | | | | 1 | 2 |

| GENUS / (Family) | ET | NO | HO | OR | AN | NE | Species number |
|----------------------|----|----|----|----|----|----|----------------|
| Tuberemaeus | 1 | 1 | | 1 | | | 26 |
| Williamszetes | | | | | | 1 | 2 |
| Xenillus | | 1 | 1 | | | 1 | 74 |
| Xiphobelba | | 1 | | 1 | | | 5 |
| Xylobates | 1 | 1 | 1 | 1 | 1 | 1 | 39 |
| Zetorchestes | 1 | 1 | 1 | 1 | 1 | 1 | 15 |
| Zygoribatula | 1 | 1 | 1 | 1 | 1 | 1 | 106 |

Results of numerical evaluations

Taxonomical indicators

From ecological and faunagenetical aspects, we considered the species number of the genera and the genus number of the families as appropriate for indication purposes among the information stemming from the taxonomical position of individual taxa. The number of subtaxa of a taxon can show the evolutionary success of the taxon, the extent of adaptive radiation, but it can also bear information on the evolutionary age or even about the geographical spread of the taxon. The subtaxon number of the higher hierarchy levels obviously stems from a more distant geohistorical past, than that of lower hierarchy levels. For taxonomic indicators, we calculated the average of number of species of genera found on individual habitats weighted by constancies (and the empirical and relative variances), and the average genus number (and variances) of the related families (Table 1). In respect of Costa Rica, Brazil and New-Guinea we found that ascending from the tropical rainforest to the top of the mountain (to the direction of mossforest and paramo vegetation) the average species numbers of genera show a gradual growth. By analyzing the empirical variance of this indicator, it can be stated that the least variance can be found at the level of rainforest. This means that members of genera with higher number of species live in higher altitudes, the highest average number of species can be found in the Costa-Rican paramo, and the least in the Costa-Rican rainforest.

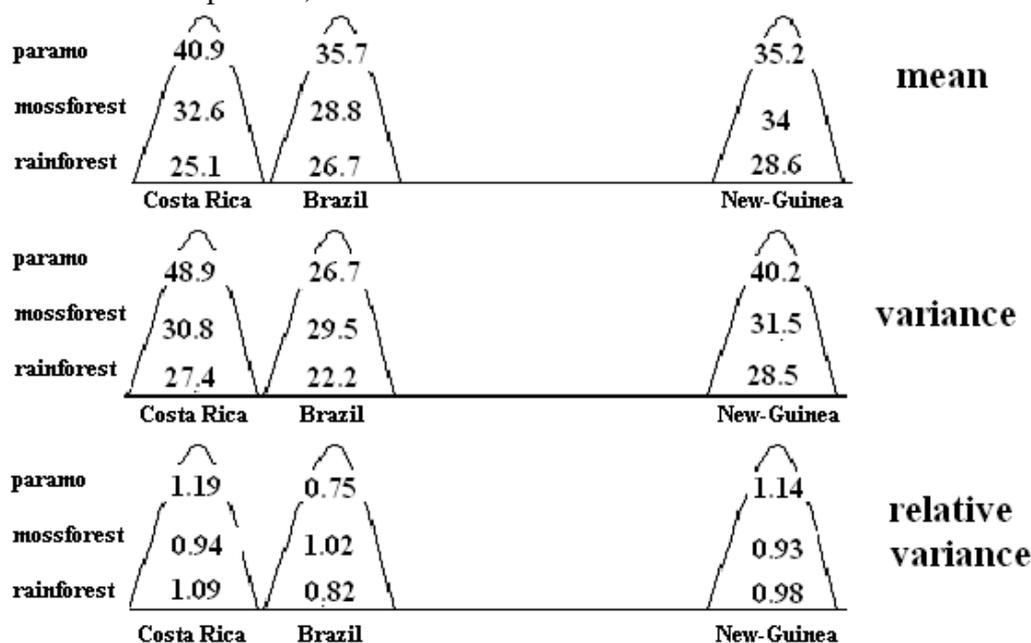


Figure 1. Average number of species and variance of genera of individual habitats

A similar analysis can be conducted by evaluating the average genus number of the families which the genera belong to (Table 2.). This indicator has been implemented to show the “taxonomical isolation” of the related genus. Figure shows that in all three examined areas, representatives of families with the highest genus number lived in the mossforest, and those with the lowest genus numbers in the rainforest. Compared to the rest of the habitats, mossforests’ genera can be characterized with the “most populous” family. Paramo always stood closer to the mossforest in this respect. Furthermore it can be stated that both the empirical and relative variances of this indicator are highest in mossforests. Comparing the areas, we can see that the average values in New-Guinea are slightly higher than those on the American continent. Lowest value can be found in the Brazilian rainforest.

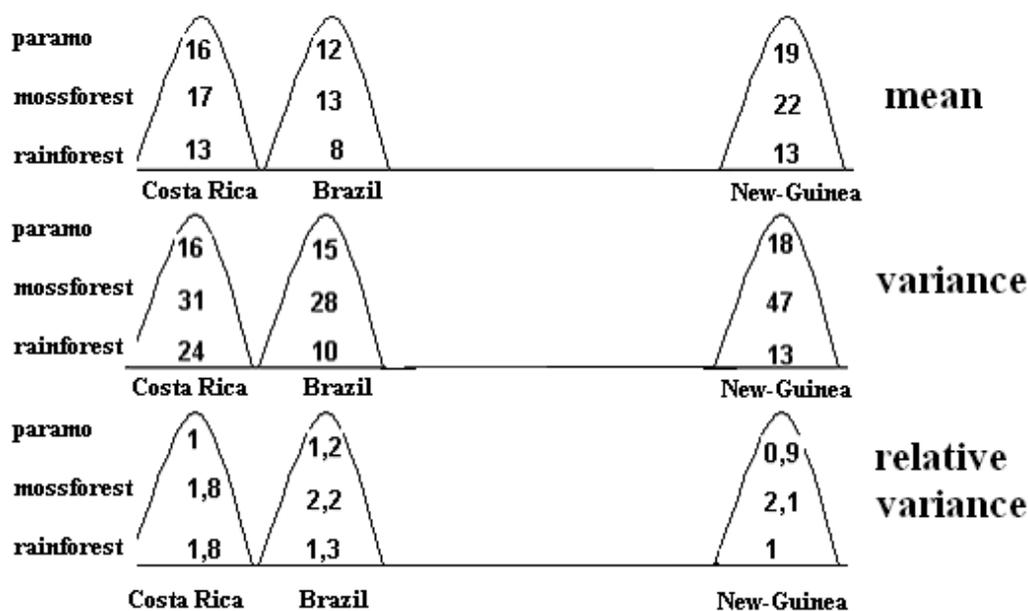


Figure 2. Average genera numbers and variance of families belonging to genera of individual habitats

Zoogeographical indicators

For the purpose of zoogeographical analysis, we used the information of worldwide prevalence of representatives of individual genera, based on the data of Table 2. We introduced the method of “simple voting” where the occurring genera give one vote on the zoogeographical regions where at least one of their representatives lives. Summing up the zoogeographical votes, the obtained score characterizes the “faunagenetical affinity” of the habitat to zoogeographical regions. Sums of obtained votes are shown in Figure 3. It can be read from the figure that Neotropis and Notogaea votes were obviously highest on their own sites, but it is interesting to observe that this value is always highest in the rainforest and it gradually decreases by ascending towards the top of the mountain. This means that in mossforests and paramos the influence of other regions (and cosmopolites) is higher. In Neotropis this phenomenon shows in the growing role of the Holarctic fauna, while in Notogaea the role of Antarctic fauna

grows. The effects of Orientalis and Ethiopis do not differ significantly from each other, which may be surprising in respect of the New-Guinean area. The effect of Orientalis is the strongest always in rainforests, while the influence of Antarctic is most significant in paramos.

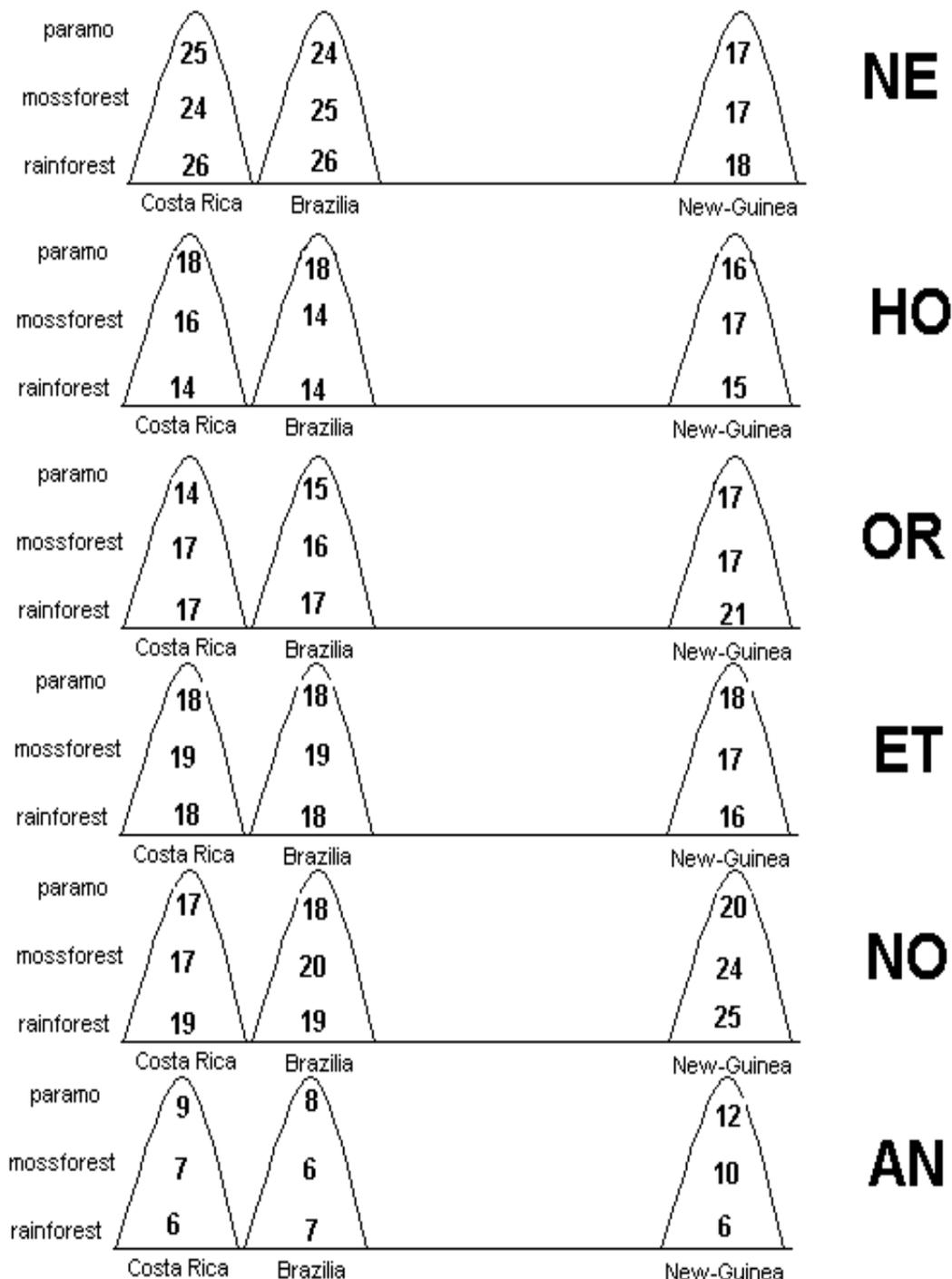


Figure 3. Sum of votes of individual sites for the world's zoogeographical regions, based on the occurrence of representatives living there

In respect of Antarctic (AN) it can be stated that with its significantly lower sum of votes it sharply distinguishes from data characteristic to other continents. Highest values can be found in New-Guinean paramos and mossforests, and high values can also be found in the paramo belt of the American continent. Low values can be observed in the rainforest and mossforest habitations of the American continent. As for Neotropis (NE), the highest values can be found in the rainforests of the American continent, and the lowest ones in the New-Guinean paramo and mossforest habitats. Based on votes of Notogaea (NO) the lowest values can be observed in the higher regions of Costa Rica. Votes of Ethiopis (ET) and Orienthalis (OR) regions seem similar, but it is clearly visible that the votes of Ethiopis are generally higher in all areas except the New-Guinean rainforest, which shows paramount Oriental influence, however the effect of Ethiopis is lower in this region. The lowest sums of votes of Orienthalis (OR) region can be found in the Costa Rican and Brazilian paramos. The highest values of the Holarctis (HO) region can be observed in the paramos of the American continent, while the lowest influence can be experienced in the rainforests.

Heterogeneity indicators

We consider as an important question of indication that in what extent the general structure of soil samples collected from different habitats differ from each other, which describes how heterogeneous coenology the site in question has generically. As a measure of heterogeneity, we chose the average pairwise difference of individual samples of identical sites, which had been evaluated by using two indicators with largely different biometrical characteristics: PHI coefficient and Jaccard function (*Figure 4*). According to the examinations, paramos were always the most heterogeneous, and mossforests were always found to be the most homogeneous. Heterogeneity of the rainforests stood always closer to the mossforests. Highest heterogeneity was shown by the New-Guinean paramo, while the lowest by Brazilian mossforest according to both distance functions.

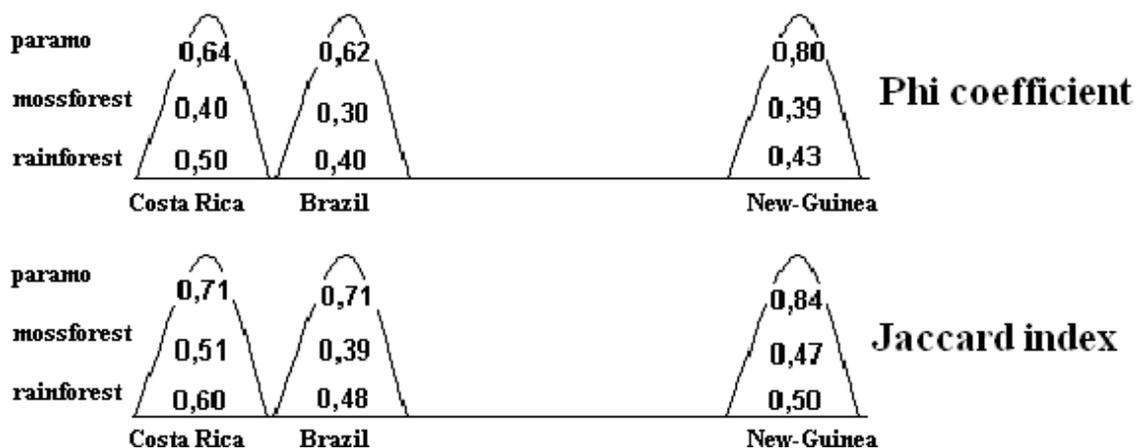


Figure 4. Generic heterogeneity of individual habitats based on the average difference of individual sample pairs

Coenological similarity patterns as indicators

Coenological similarity patterns can be analysed on multiple spatial scales (scale levels). We also analysed the similarity patterns of generic lists of different sites by NMDS with Euclidean distance, and hierarchical cluster-analysis. The two analytical results are shown projected onto each other (*Figure 5*). The multivariate similarity pattern of habitats' Oribatid community gave the expected picture. It can be stated that differences originating from the habitats and continents can also be recognized in the similarity patterns of the generic lists of the examined habitats. However, it can seem surprising that despite the vast geographical distances the pattern generating role of habitats does not disappear, it seems perhaps even more important. In accordance with the real ecological conditions, mossforest plays a transitional role between rainforest and paramo. However, mossforests are the most similar to each other and they are positioned in the middle of the similarity pattern, while the rest of the sites are separated radially. It is clearly visible that Brazilian sites are much more similar to each other than the Costa-Ricans.

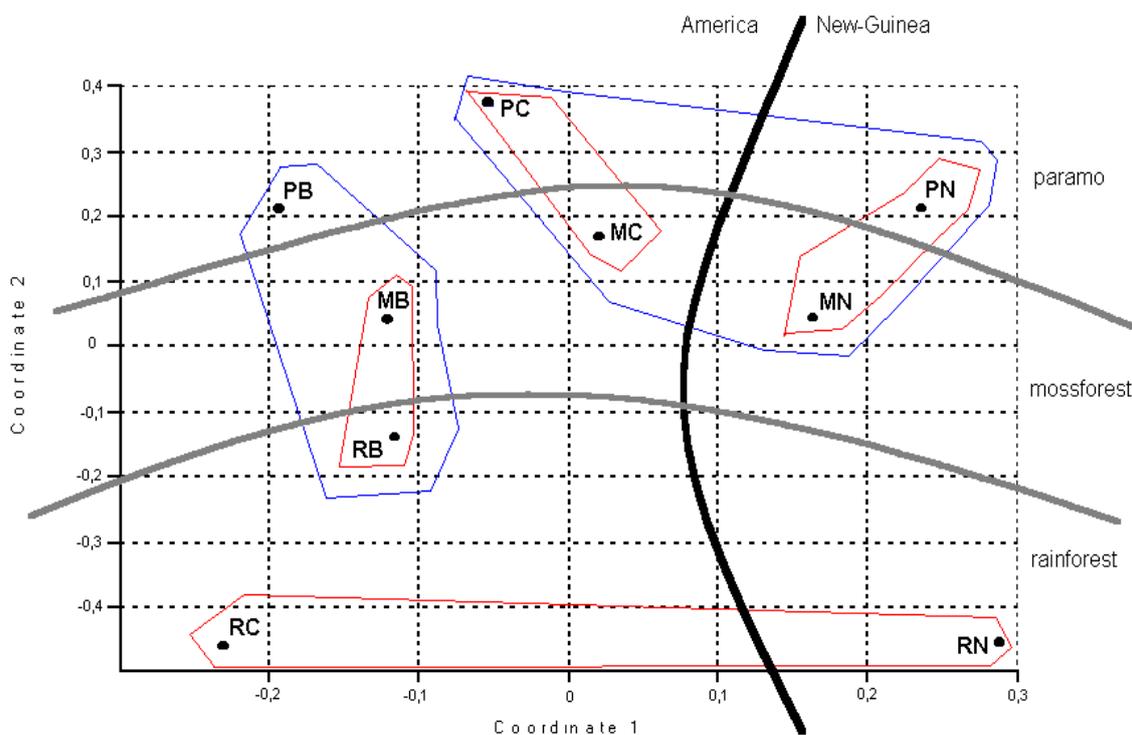


Figure 5: Similarity pattern of the examined sites in an NMDS ordination with the projection of the hierarchical cluster analysis results, applying Euclidean distance.

Comparison of the sites can be fine-tuned if we also examine the similarity pattern of the individual soil samples considering every sample as different objects independent from the sites. We analysed this similarity pattern also by applying NMDS and Euclidean distance (*Figure 6*). Analysing the collective similarity pattern of every individual sample it can be stated that the groupings of elementary samples reflect their relations to the sites. This justifies the methodological decision by which sites are considered the basic objects of the examination. It can be stated furthermore, that habitat-type is unambiguously more significant pattern-generating factor than

geographical attribution. Rainforests, mossforests and paramos lying thousands of kilometers from each other are more similar than sites of other habitats at only a few kilometers distance. Following the results of these pattern analyses, exact examination of the observed phenomena with a regression model seems to be practical.

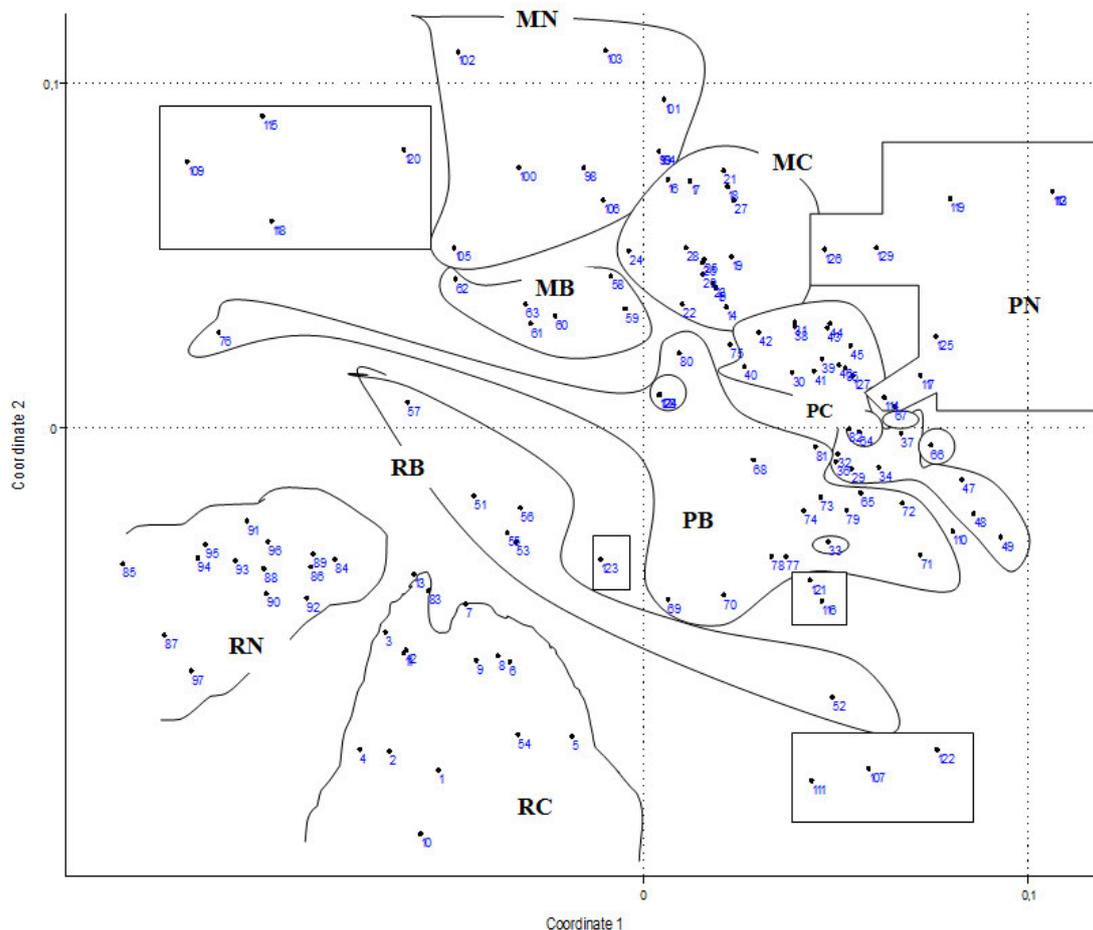


Figure 6: Similarity pattern of elementary samples in an NMS ordination by applying Euclidean distance.

With the help of the tools of regression modelling we tried to describe what kind of factors and in what extent explain the occurrence of Oribatid genera.

For the purpose of exact statistical examination we classified the 82 individual soil samples into groups by habitats, habitat-types and continents. We distinguished samples originating from the identical site, identical habitat (habitat-type) and identical geographical unit. Samples from different geographical units were allocated into two groups depending whether they were collected from identical or different habitat-types. For the purpose of identifying the pattern generating factors we created criteria for the statistical evaluation based on this classification as follows:

| Criterion | Number of samples |
|--|--------------------------|
| In-site | 9 |
| Inside habitat | 9 |
| Inside continent | 9 |
| on other continent | 12 |
| on other continent from neighbouring habitat | 6 |
| Total | 45 |

During the statistical analysis we based our calculations on 45 distance values which were created by the following method: the 82 samples contained 111 Oribatid genera. Consequently we characterized every sample with a column vector of 111 elements. The elements of these vectors were created as follows:

- 1: on those places, where the given genus is present in the sample
- 0: on those places where the given genus is not present in the sample.

With the help of the binary data created this way, we intended to examine how 'similar' two samples are. There are many indices in biometry for similarity (Podani 1997), since the task of biological examinations is often the numerical measurement of an intuitively defined similarity. In case of binary data sets, there are many possibilities to measure similarity. For the analysis we used the product moment correlation (PHI) coefficient. This coefficient was created with the help of the Syntax program, for every sample. This resulted in a distance matrix, where the elements of the matrix are the values of PHI coefficients calculated between the two samples.

During sample collection, researchers have taken many samples from a habitat, thus one habitat is characterized by many samples. In order to filter out the sample-specific effects, we took random samples consisting of 6 elements from the calculated distances for each examined criterion. The criterion has been characterized by the average and variance of these 6 values:

Table 3. Statistical characteristics of criteria.

| Criteria | Number | Average | Variance | Relative variance |
|---|---------------|----------------|-----------------|--------------------------|
| in-site | 9 | 0.612 | 0.011 | 1.82% |
| in the same habitat | 9 | 0.864 | 0.008 | 0.87% |
| in the same geographical unit | 9 | 0.894 | 0.003 | 0.38% |
| on other geographical unit | 12 | 0.976 | 0.004 | 0.44% |
| on other geographical unit. in a neighbouring habitat | 6 | 1.002 | 0.003 | 0.28% |
| Total | 45 | 0.883 | 0.006 | 0.63% |

Further analysis consisted of two parts. First, with the help of graphical analysis (*Figures 7 and 8*) we set the starting hypotheses, and then numerically measured the suspected effects with multivariate regression and examined the significance of the obtained conclusions.

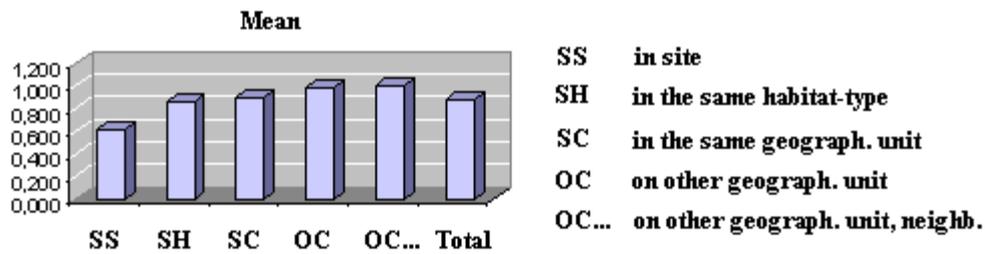


Figure 7. Average distance/similarity of criteria.

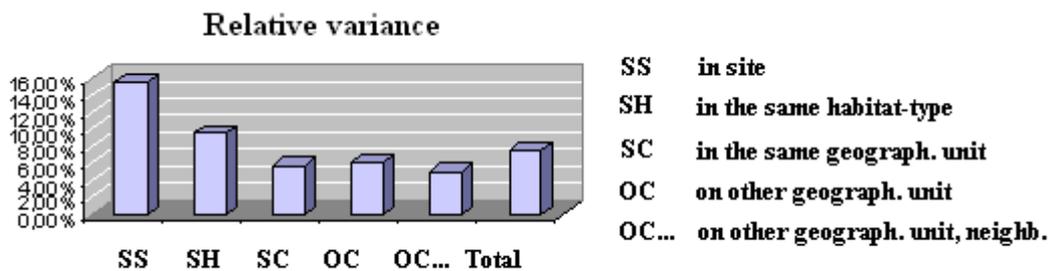


Figure 8. Relative variance of distance/similarity of criteria.

Based on *Figures 7 and 8*, it seems that the difference between in-site samples is significantly less than that of between other samples. On one hand, this affirms sample collection and, on the other hand it reaffirms the decision of the researchers selecting genus as the basic unit of analysis. The variance of in-site samples is significantly higher than that in other cases. Based on the figures the null-hypothesis can be supposed that the difference is significantly less in-site. Between geographical units, the distance of samples seems significantly higher than in the case of samples on identical geographical units. The question emerges whether the geographical unit or the habitat type defines better the distance between the samples. Are genera inside a habitat significantly more similar than in case of samples collected from the same geographical unit but from different habitats? We tested these null-hypotheses by using uni- and multivariate statistical tests.

First, we are going to interpret the result of the univariate model and then improve the model by implying more variables.

We conducted the test by using the Eviews statistical program. During the examination, we checked by using the t-test whether the given variable is significant or not. The null-hypothesis of the test was that the coefficient belonging to a given variable was zero. Instead of t values, we used p (marginal significance coefficient) values in the tables, which show the probability of rejecting the null-hypothesis. The advantage of using p values is that there's no need to work with a pre-set level of significance, instead, the probability of beta error can be reduced according to the estimation.

First, we examined if there's significant difference among the average distances between the samples grouped by different criteria. We tried to check the null-hypothesis by using linear regression. In case of every regression, the null-hypothesis was that the distance of the sample grouped by a given criterion differed significantly from the average distance characteristic to the samples. Hypotheses could be tested by using dummy-variables. For example:

site = 1, in case of sample taken from the identical site

site = 0, in case of sample taken from a different site.

The average distance of samples is marked by: distance. In this case, the estimating equation:

$$(1.) \text{ distance} = \beta_0 + B_1 * \text{site}$$

if, for example the t-statistic belonging to β_1 is significant, then the location of sample collection explains the distance. By implementing similar dummy-variables, the estimation to characterize continents and habitats can be made.

Table 4. Dummy variables defined for the examination

| Criterion | Dummy |
|---|------------------|
| in-site | SITE |
| inside the habitat | HABIT |
| inside the geographical unit | CONTINENT |
| on other geographical unit | NOCONTINENT |
| other geographical unit on a neighbouring habitat | NOCONTINENT2 |
| Calculated similarity of the samples: | DISTANCES |

The results of the estimation are summarized in Table 5. C(1) marks the constant in every case.

Table 5. Result of univariate linear regression estimations

| Dummy variable | Estimating equation | C(1) | C(2) | Significance level | R-square |
|----------------|--------------------------------------|------|-------|--------------------|----------|
| Site | DISTANCES = C(1) + C(2)*SITE | 0.94 | -0.32 | 0.00 | 0.60 |
| Habit | DISTANCES = C(1) + C(2)*SITE | | | 0.68 | |
| Continent | DISTANCES = C(1) + C(2)*CONTINENT | | | 0.55 | |
| Nocontinent | DISTANCES = C(1) + C(2)*NOCONTINENT | 0.85 | 0.13 | 0.01 | 0.14 |
| nocontinent_2 | DISTANCES = C(1) + C(2)*NOCONTINENT2 | 0.86 | 0.14 | 0.04 | 0.10 |

Based on the results above, we can clearly see that the distance between samples taken from identical sites is significantly less than that in the case of other samples. This means that the examined genera statistically characterize a given habitat. Otherwise: when comparing two soil samples it can be determined whether they are from the same site or not by the examination of Oribatid genera. Thus the examined animals can be used for indication purposes.

Further results show that the distance of samples between geographical units is greater in average than that in the case of identical geographical units. However we can't be sure that this result is caused because the samples collected from the same site belong to the identical geographical unit, and these samples significantly reduce the average difference. In a similar way, it can also be supposed that the distance between the samples belonging to the same habitat is not significant because the distance is biased by the effect of samples from the same site. This is why we re-estimated the regressions in such a way that the site dummy would have been included in every regression. The results of the estimation are summarized in *Table 6*:

Table 6. Result of bivariate linear regression estimates

| Dummy variable | Estimating equation | C(1) | C(2) | Significance level | C(3) | Sign level | R-square |
|----------------|--|-------|--------|--------------------|--------|------------|----------|
| Habit | DISTANCES = C(1) + C(2)*SITE + C(3)*HABIT | 0,960 | -0,348 | 0,000 | -0,096 | 0,010 | 0,665 |
| continent | DISTANCES = C(1) + C(2)*SITE + C(3)*CONTINENT | 0,944 | -0,332 | 0,000 | | 0,399 | 0,611 |
| nocontinent | DISTANCES = C(1) + C(2)*SITE + C(3)*NOCONTINENT | 0,916 | -0,304 | 0,000 | 0,060 | 0,089 | 0,632 |
| nocontinent 2 | DISTANCES = C(1) + C(2)*SITE + C(3)*NOCONTINENT2 | 0,923 | -0,310 | 0,000 | 0,079 | 0,076 | 0,634 |

Based on *Table 6* it can be stated that the site dummy is also significant at 1 % level in every case. This affirms the result that the genus-level classification of Oribatid genera is sufficient, and furthermore, their distribution characterizes a soil sample in a statistically significant manner. So these genera can be well used for biological indication.

Among further dummy variables, the variable characterizing the habitat is significant even at 1 % level. This means that two samples collected from the same habitat are more similar than two other kinds of samples. Thus, the habitat characterizes the distribution of the genera more significantly than the geographical unit the sample originates from. In case of different geographical units, the difference between the samples is only significant at 10 % level of significance. This is why the acceptance of this hypothesis greatly enhances the probability of beta error.

Following the aforementioned methodology, proceed from the simple towards the complicated and repeat the estimation with the joint application of variables characterizing habitat and geographical unit (*Table 7*).

Table 7. Result of regression estimates using three variables

| Dummy | Estimating equation | Coefficient | Significance level | R-square |
|-----------|--|-------------|--------------------|----------|
| C | DISTANCES = C(1) + C(2)*SITE + C(3)*HABIT + C(4)*CONTINENT | 0.984 | 0.000 | 0.697 |
| SITE | | -0.372 | 0.000 | |
| HABIT | | -0.121 | 0.002 | |
| CONTINENT | | -0.073 | 0.052 | |

Table 7 shows that all variables in the model are significant at 6 % level. Thus, by accepting the model specification, the probability of beta error is limited. The average value of the difference of two random samples is **0.984**. If these samples are collected from the same continent, this difference is by **0.073** lower, and if the samples are from the same habitat, this difference is by **0.121** lower than the average value. An interesting result is that the distribution of genera is heavier influenced by the habitat type than the geographical unit (the size of which, in our case is practically of continent scale). If samples are from the same site, the average distance is by **0.0372** smaller than the average value. Model explains 70 % of the deviation from the average.

To check the specification of the final model, we examined the distribution of the error components. An important condition of the statistical analyses grounding the final result is the normal distribution of error components. We checked the normal distribution of error components with two kinds of methods. First, we displayed the distribution graphically, and then checked the distribution of error component with the Jarque-Bera test. This test compares the difference between **skewness** and **kurtosis** with that of normal distribution. The null-hypothesis in this case was that the distribution of the samples is normal. The displayed probability shows the level of significance at which we could reject the null-hypothesis.

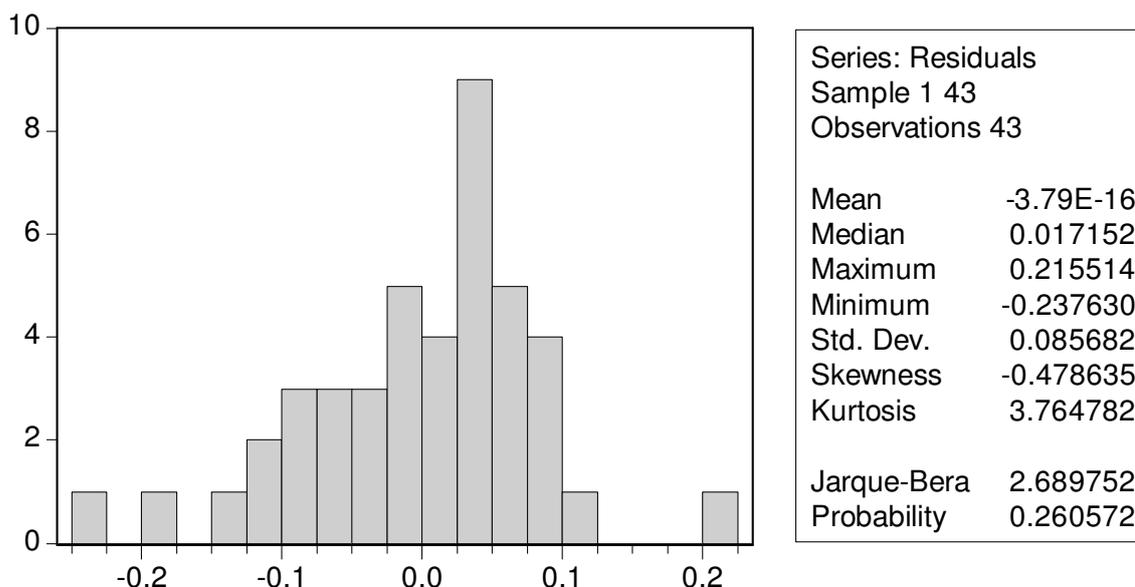


Figure 9: Examination of error coefficient of the final model.

As *Figure 9* shows, the distribution of error coefficient converges well to normal. We can not reject the null-hypothesis of the normal distribution even at 10 % level. Thus we accept the model in its final form.

Theses

1. We pointed out that the average species number of those genera where the present Oribatids belong to, can be properly used for the characterization of habitats Concerning Costa Rica, Brazil and New-Guinea, we found that this indicator shows a continuous growth advancing upwards from the tropical rainforests (towards the belt of mossforests and paramo vegetation). Examining the empirical variance of this indicator, it can be stated that the least variance can be found at the level of rainforest in every case. This means that members of genera with greater species numbers live at higher elevations.
2. The average genus number of families of Oribatid genera present at individual habitats also proved to be a useful indicator. We pointed out that in case of all the three examined locations, representatives of families with the greatest genus numbers live in the mossforest, and representatives of families with the lowest genus numbers live in the rainforest. In this respect, paramo always stood closer to mossforest. Furthermore, we pointed out that the relative and empirical variation of this indicator is the greatest in the mossforest.
3. Concerning zoogeographical indication, we pointed out that the method of “simple voting” can result in well-interpretable indicators in respect of the generic relativity of individual habitats and main zoogeographical regions. Votes of Neotropis and Notogaea were highest in their own sites of course, though interesting that this value is always the highest in the rainforest and gradually decreases advancing upwards the hill. This means that the influence of other regions (and cosmopolites) is greater in the mossforests and paramos. This phenomenon manifests in Neotropis in the growing influence of Holarctic fauna, and the growing influence of Antarctic fauna in the Notogaea. The effects of Orientalis and Ethiopis do not differ significantly, which can be surprising in respect of the New-Guinean location. However, the effect of Orientalis is always the strongest in rainforests, while paramo has the strongest Antarctic influence. But the small difference between the votes calls for the usefulness of later inclusion of new taxa.
4. Examining the proportion of species below 20 % and 40 % constancy, we pointed out that these indicators are always the highest in paramos.
5. We pointed out that the information on the extent of heterogeneity of the genus composition of the soil samples of an individual habitat can be well used in the characterization of the habitat. Evaluating by PHI coefficient and Jaccard function the average pairwise dissimilarity of the individual samples from identical sites as the measure of heterogeneity, we always found the paramos to be the most heterogeneous, and always the mossforests to be the most

homogeneous. The heterogeneity of the rainforests always stood closer to that of mossforests’.

6. We pointed out that dissimilarities of habitats caused even by their type and also by the continent they originate from can be recognized in the similarity pattern of genus lists of the examined habitats. But if we analyze the overall similarity pattern of all the individual samples, it is quite conspicuous that the type of habitat is a much more significant pattern-generating factor than the geographical location. Rainforest, mossforests and paramos located many thousand kilometers from each other are more similar to each other than sites of other kind of habitats in only a few kilometers away. This statement is even statistically verified by the multivariate linear regression fitted to our data.

Discussion and conclusion

The most important result of our case study is that the list of Oribatid genera as a coenological indicator, primarily characterizes the present ecological effects of the habitat and its climatically determined type of vegetation; and represents the effect of zoocoenological past in a much lesser extent. Thus, it can be concluded that a meritable scientific faunagenetical analysis should not be based upon geohistorical, but climatological grounds. This is why the ecological indication based on Oribatid genus lists provides unique possibilities for the purpose of climate change research.

It became obvious that if we had chosen species and not genera as the basis of our examination, we would not get results that were interpretable from bioindicational aspect. This is because the majority of the described species would have appeared only as local specifica, and they do not provide any meritable information on similarity patterns – unless we are thinking in a very small grade of space. Species-level indication studies would be only rational in the case if we would deal only with cosmopolite species, but their number and detectability would not be sufficient for the majority of examinations for practical tasks. Thus, our important conclusion is that under current circumstances, the recommended taxonomical unit for indicational ecological studies can only be the genus. This statement is also important because many authors (primarily species describing taxonomists) consider a serious problem of indicational research that a number of researchers classify individuals only to genus level (Gulvik 2007). However, based on the work of Caruso (2006), we know that human contamination, intervention and disturbance can be better detected if we examine larger taxonomical units. It is also clear that rapid changes can not be detected on species-, but on community level. From the same work, it is also known that the species data of Oribatid mites can be raised to genus- or family level, and this does not cause loss of data or sensitivity by multivariate methods. According to Osler (1999), it is possible that habitat preference is determined rather at family level. Furthermore it is also known that there is strong relation between species-level and higher taxon level diversity indicators.

At the same time, the standardization and quantification of current Oribatid-collection methods would be obviously necessary for the development of the bioindicational methodology in order to make the data from different authors comparable. The need for this is emphasized more and more in literature (Gulvik 2007). A criteria-system of classifying the collected individuals into genera (or into other optional morphological groups) can be considered as a part of the standardized method.

The current identificational and taxonomical practice in oribatodology is almost completely unsuitable for the purposes of biological indication research. Till such methods are unavailable, case studies can be conducted only if the person doing field sample collection and taxonomical processing is identical, and furthermore, this is only true if the coenological matrices have been created with the greatest care.

During our examinations, we pointed out that by advancing vertically upwards in the tropical high mountains (from rainforests towards the paramo vegetation), the average species number of genera present, and the extent of Holarctic and/or Antarctic relations of present genera grow, which can be well interpreted with the conception system of geographical analogy based on climatic similarities. This indication adequately supports former studies on the role of vegetational similarities and on genera as taxonomical units suitable for indication. Many authors (Andrew 2003, Melamud 2007) state that advancing upwards on the mountains, elevation above sea level and exposure have significant influence on the diversity of Oribatids. Besides, it is known that Oribatid diversity grows from the Boreal region towards warmer climates, but it does not grow further towards the tropics (Maraun 2007).

Furthermore, we pointed out that from the aspect of similarity of individual samples, among the examined habitat types the mossforest is the most homogeneous habitat, and paramo is the most heterogeneous. This latter phenomenon can be well interpreted if we consider the uniform moss cover prevalent in the mossforest, and the role of stable microclimate created by the moss cover. In the paramo, the observed proportion of species with low constancy level and also the heterogeneity of habitats (tussocks with different size) are high, and the role of the resulting microclimatic variability is obvious.

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