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Two scale patterns of spatial distribution of oribatid mites (Acari, Cryptostigmata) in a Greek mountain

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Summary

In this paper we describe and compare the oribatid distribution patterns at two scales: a regional scale corresponding to an altitudinal gradient and a local one created by the variation of vegetation cover. Distribution patterns at the local scale are assessed by sampling under the canopy of the *Juniperus* sp. shrubs, which are scattered all along the altitudinal gradient, and at the adjacent grass-covered openings. Our results showed that the two scale effects are not equally important in shaping the oribatid communities. Altitude *per se* does not induce clear distribution patterns, acting mostly indirectly through the effect on the formation of local vegetation. In contrast, profound differences in the structure of oribatid communities are imposed by the local scale effect, which consists of strong microclimatic fluctuations in the exposed grassy sites and litter accumulation in the sheltered shrubby sites. Oribatids respond to the two scale effects, forming separate communities with distinct characteristics. The temporal heterogeneity of the exposed habitats at all altitudes leads to a temporal separation of oribatid niches and to a seasonal succession of communities. The structural heterogeneity of the shrubby habitats is responsible for a more complicated and site-specific differentiation of communities; oribatid species of shrubby sites are either capable of inhabiting the open sites as well or persist throughout the whole year.

Key words: Elevation gradient, altitude, regional effect, local effect

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Introduction

The spatial distribution of oribatid mites has been a prominent research topic in soil biology for many decades. Spatial distribution patterns have been described at a range of scales from local to latitudinal gradients (Usher 1975; Anderson 1978a; Schenker 1984; Stamou & Sgardelis 1989; Asikidis & Stamou 1991 among others). All of these studies focus on the concept of diversity, since it describes the complexity of biocenoses and allows comparisons of different sites (Schatz 1998).

Oribatid distribution patterns at fine local scales have been studied for a variety of ecosystems. These patterns are determined by biotic and abiotic factors, like intraspecific relationships, food availability, soil temperature, humidity, pH and microhabitat architecture (Butcher et al. 1971; Anderson 1978a; Mitchel 1978; Schenker 1984; Tousignant & Coderre 1992; Sgardelis & Usher 1994; Hansen & Coleman 1998).

So far there have been only a few studies on the effect of altitude on the distribution of oribatid mites (Walter 1985; Lamoncha & Crossley 1998; Schatz 1998). In these studies, the observed patterns depend to a great extent on landscape properties operating at small scales. Wagenet (1998) as well as Heneghan & Bolger (1998) emphasize the difficulties of extrapolating information on the structure and function of soil systems from one scale to another, due to the multiple interacting factors that affect soil processes.

In this paper we describe and compare the oribatid distribution patterns at two scales, a coarse regional and a fine local one. The regional scale is the altitutinal gradient of Mt. Vermion (Macedonia, Greece). In order to minimize heterogeneity due to local vegetation and the resulting soil structure, we focused on the oribatid communities associated with the litter of *Juniperus oxycedrus* at low altitudes and *J. communis* at high altitudes. Thus, we assess distribution patterns at the local scale by sampling under the canopy of the *Juniperus* sp. shrubs and at the adjacent grass-covered openings.

Our interest is focused on identifying the relative importance of the two scales in shaping the oribatid species assemblages. More specifically, we compare the effects of vegetation cover and altitude on abundance, species richness and community structure of oribatid mites.

Materials and Methods

Study site

The study took place along an altitudinal gradient of Mt Vermion, about 150 km southwest of Thessaloniki. Samples were taken from four stations along the eastern slope of the mountain (Table 1). The selected stations differed in many aspects, such as climate, vegetation structure, litter accumulation and structure of soil layers. However, all stations are characterized by the presence of *Juniperus* sp. shrubs. These shrubs were distributed along the altitudinal gradient, being either dominant or among the most dominant species of the woody plant communities at all stations. They belonged to the species *J. oxycedrus* at low altitudes and *J. communis* at the high altitudes (the shrubs are referred to by the generic name hereafter). Litter was well retained under their cushion-formed canopies and the organic layers were of similar structure at all sampling stations. Thus, in order to distinguish the altitudinal effect from possible effects imposed by litter quality and topsoil structure, we selected sampling microsites that were similar in all sampling stations, i.e. under the canopy of the *Juniperus* sp. shrubs and at the adjacent grass-covered openings.

Table 1. Sampling stations and microsites along the altitudinal gradient. The altitude and the dominating woody species, as well as the microsite codes are indicated (J: under the *Juniperus* sp. canopy, O: outside the *Juniperus* sp. canopy)

Station	Altitude (m asl)	Vegetation	Microsite codes
A	450	Mediterranean ecosystem (*Quercus coccifera* dominating)	AJ, AO
B	700	Temperate forest clearing (*Juniperus oxycedrus* dominating)	BJ, BO
C	900	Deciduous woodland (*Carpinus orientalis* dominating)	CJ, CO
D	1150	Alpine meadow (Juniperus communis dominating)	DJ, DO

Sampling

Soil samples were collected with a steel cylinder (5.4 cm diameter) at monthly intervals, from April 1994 to March 1995. At each of the four sampling stations, we took three samples from randomly selected *Juniperus* shrubs and three from the adjoining grass covered openings (6 samples per station, 24 samples per month). Each soil core (sample) consisted of the top 7 cm of soil that contained the whole organic layer in every case. Sampling was impossible during December, and in some cases during January, due to excessive snow cover, which restricted the access to the area. On all sampling occasions, soil temperature and water content were measured. Temperature was measured by min-max thermometers placed 1cm below surface in the *Juniperus* litter and in the adjoining grass-covered openings and left in the field for the whole month. In order to assess the water content (% dry weight), three soil samples taken from each microsite were weighed, oven dried to constant weight (104 °C for one day), and weighed again.

Animals were extracted from samples by means of a modified Berlese-Tullgren apparatus and collected in a 70 % alcohol solution, in which 5 % glycerin was added. Only mature individuals were considered, which were identified to morphospecies level.

Data analysis

For assessing the diversity of oribatid communities in the different microsites, we used the method of diversity ordering proposed by Renyi (1961). Renyi's parametric index of order *a* is an extension of Shannon's entropy and is given by the formula

$$H_a = \begin{cases} \dfrac{log \sum_{i=1}^{S} p_i^a}{1 - a} & \text{for } a \neq 1 \\ -\sum_{i=1}^{S} p_i \, log \, p_i & \text{for } a = 1 \end{cases}$$

where p_i is the fraction of the population abundance corresponding to species i, S is the number of species and a is the scale parameter, i.e. an arbitrary positive real number. The index shows varying sensitivity to the rare and abundant species of a community, as the scale parameter a changes (Ricotta 2000). Plotting the value of the index against the scale parameter provides the diversity profile of a community. For $a = 0$, the index equals the logarithm of species number, i.e. all species, even the rare ones, contribute equally to the diversity of the community. For $a = 1$, the index equals Shannon's diversity index. For $a = 2$, the index equals Simpson's diversity index. For a tending to infinite, the index is most sensitive to the abundant species. Thus, when the curves of two diversity profiles differ in the range of low a values, this is due to the number of species. In the range of high a values, differences are due to the presence of abundant species. When two diversity profiles intersect, the two communities are considered non-comparable, i.e. they may be ordered differently by different diversity indices. For the calculations we used the DivOrd program created by Tothmeresz (1995). We preferred this method of diversity ordering to any of the known diversity indices, as it is a family of indices that includes the most widely used ones. Different indices emphasize different aspects of diversity producing inconsistent ordering of communities. These inconsistencies are unavoidable whenever one attempts to reduce a multidimensional concept, such as a community, to a single number.

For the clustering of our samples we used both a hard and a fuzzy classification method. The former was the complete linkage amalgamation rule, based on the squared Euclidean distances among samples. In this method, we have compared microsites based on data of mean annual abundance of species. The second classification method applied was the Fuzzy c-means algorithm, developed by Equihua (1990). The method is non-hierarchical and produces clusters that overlap (fuzzy clusters) to a degree relative to a fuzziness parameter set by the user (set to 2 in our case). Each element (sample) is associated to each cluster by a membership value, which lies within the interval [0,1] and measures the similarity between an element and the semantic description of the cluster (Bezdek 1987). The method is appropriate in order to approach both the concept of communities as recognizable entities, and the concept of composition changes along a continuum (Equihua 1990). The method was used to classify in different clusters the monthly samples taken during the whole experimental year (8 microsites x 11 months), based on monthly abundance data of each oribatid species at each microsite. For the selection of the number of clusters to be formed, we used as criterion the maximization of the partition coefficient, i.e. the between to within cluster variance. In order to reduce noise arising from sampling inefficiency, we based this clustering process on ordination results (the first five axes of Correspondence Analysis) rather than on the original data.

Results

Soil water content and temperature

No significant difference of either temperature or soil water content may be attributed to altitude, although the water content recordings of the deciduous woodland at station C were higher than those of the other systems. For this reason and for saving space, instead of presenting the monthly records of abiotic variables in all sampling stations and microsites, in Figures 1 and 2 we present the difference between sheltered microsites, i.e. under the *Juniperus* canopy, and open ones.

As shown in Figure 1, the difference of soil water content of sheltered microsites minus that of open ones was positive in most cases. Thus, the soil water content under the *Juniperus* canopy was higher than in the grass covered openings in almost all cases in the high altitudes and in most cases in the low ones. This difference seldom exceeded 10 %.

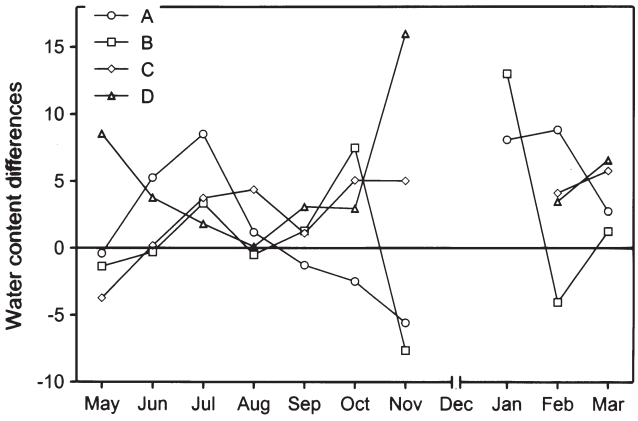
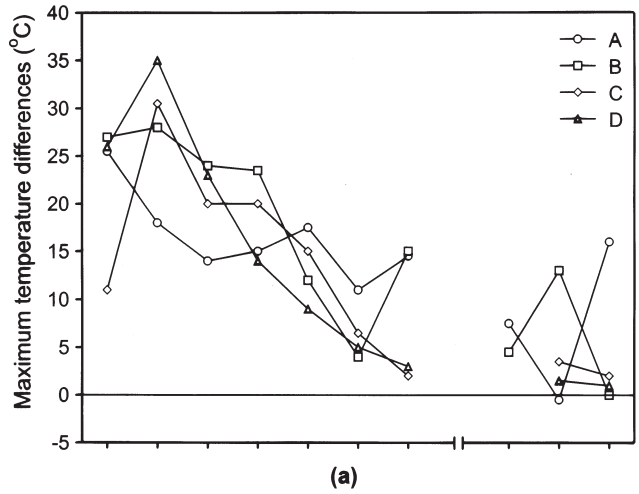


Fig. 1.
Monthly variations of % water content difference between microsites (sheltered minus open) in the four sampling stations



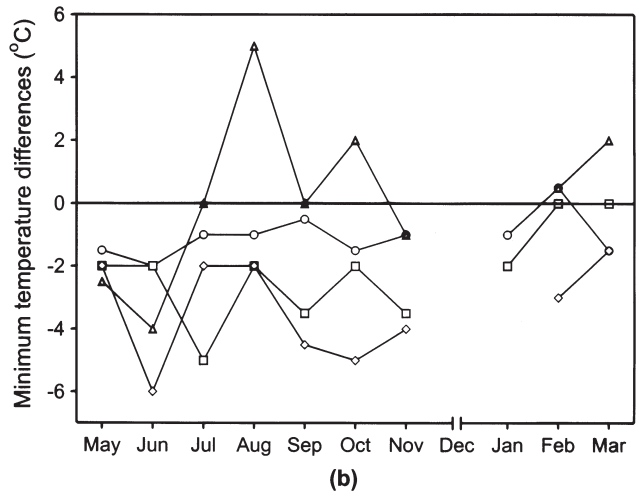


Fig. 2.
Monthly variations of temperature difference between microsites (open minus sheltered) for the period between samplings.
(a) maximum soil temperature and (b) minimum soil temperature

Higher maximum temperatures were recorded in the open microsites in comparison to the sheltered ones (Fig. 2a). This was more obvious during the warm period of the year, e.g. in June the maximum monthly temperature in the grass covered openings of station D was 35°C higher than the maximum temperature recorded under the shrub canopy. Respectively, minimum monthly temperatures were lower in the open microsites (Fig. 2b), but the differences were not so pronounced.

Abundance, species number and diversity

At all altitudinal stations, oribatids were more abundant in the *Juniperus* litter rather than in the open microsites (Table 2). Moreover, there was no linear relation between abundance and altitude. Maximum numbers were observed in the middle of the gradient and mostly in the deciduous woodland of station C.

Fifty-seven oribatid species were collected from all microsites (Table 3). The number of species per microsite varied from 15 to 34. Twenty-five species were found exclusively in the sheltered microsites (44 % of total) and 12 exclusively in the exposed ones (21 % of total). At all stations, species richness was higher under the *Juniperus* canopy, while altitude did not seem to induce any specific pattern of changes. Maximum number of species was observed at station C.

The diversity profiles of the oribatid communities inhabiting the different microsites are given in Figure 3. In all altitudinal stations, the diversity profiles of the sheltered microsites were characterized by high scores at low values of scale parameter a and by a sharp decline of the curve for higher values of α, indicating a species rich community with few dominant species and many rare ones. On the contrary, diversity in the open microsites was lower for low values of α and declined more smoothly, indicating fewer species being equally abundant. When comparing the communities from the different altitudes, the ones inhabiting the microsites of station C (CJ, CO) were evidently the most diverse, exhibiting higher values of Renyi's index regardless the changes of the scale parameter.

Table 2. Mean annual abundance (individuals/m^2) of oribatid mites at each microsite

Station	J	O
A	39275	28550
B	63913	32173
C	71811	58188
D	57681	37391
Average	58170	39075

Table 3. Number of oribatid species at each microsite, and total number of species recorded at each station and at each microsite type along the altitudinal gradient

Station	J	O	Total per station
A	27	23	31
B	21	15	24
C	34	26	40
D	30	16	34
Total per site	48	35	

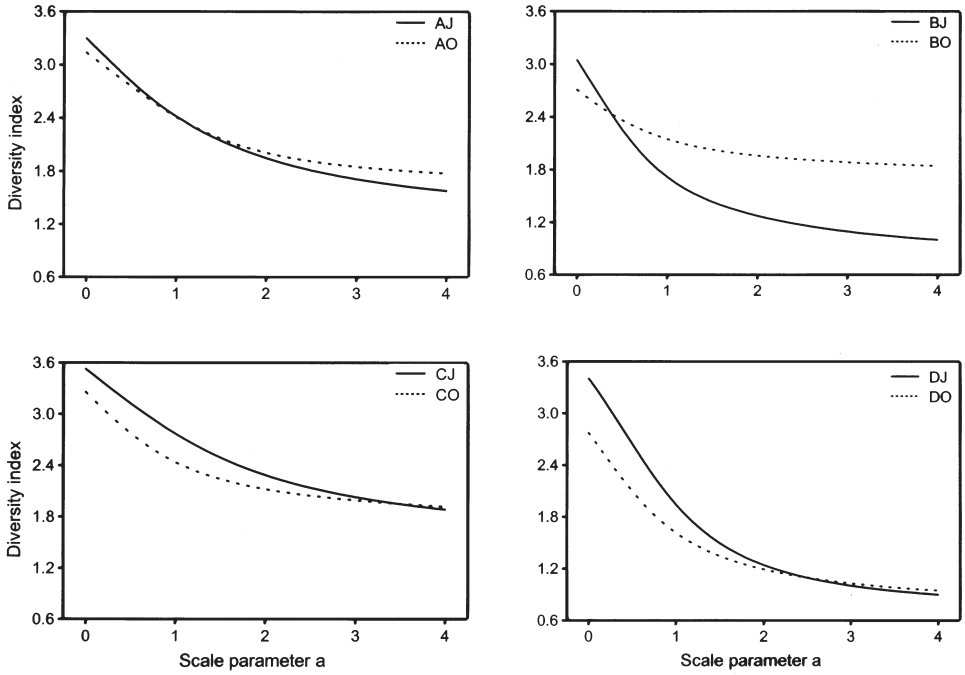


Fig. 3. Diversity profiles of oribatid communities per station and microsite. For microsite codes see Table 1

Community structure

The dendrogram of Figure 4 shows the clustering of the microsites, on the basis of mean annual abundance of oribatid species. The oribatid communities of the open microsites appear to be quite similar to each other, but distinct compared to most of the communities inhabiting the *Juniperus* litter. Moreover, their similarities display a pattern that more or less corresponds to their position along the altitudinal gradient, i.e. the open microsites of the two lower altitudes (AO, BO) were similar to each other, less similar to those of the third altitudinal station (CO), and even less similar to those of the higher altitude (DO). This does not hold for the communities under the *Juniperus* canopy, where no particular pattern was obvious.

The ordination of monthly samples from all microsites along the two first axes of Correspondence Analysis is depicted in Figure 5. The eigenvalues of the first and the second ordination axis are 0.584 and 0.551 respectively. A distinction between sheltered and open microsites is obvious. The samples taken under the shrubs are spread throughout the plane and mostly along the first axis, while the samples from the grass covered openings form a more compact group at the left part of the plane, being spread mostly along the second axis. The microsite effect is more pronounced in the high altitude stations C and D, since the samples from microsites CJ and CO occupy the endpoints of the first axis, while the samples from microsites DJ and DO are also

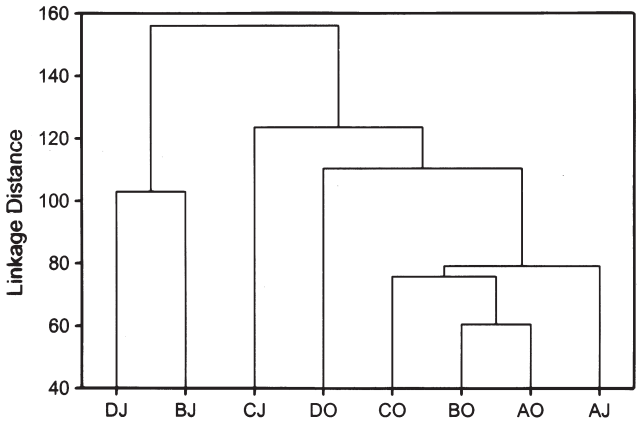


Fig. 4. Complete linkage clustering of microsites according to mean annual abundance of oribatid species. For microsite codes see Table 1

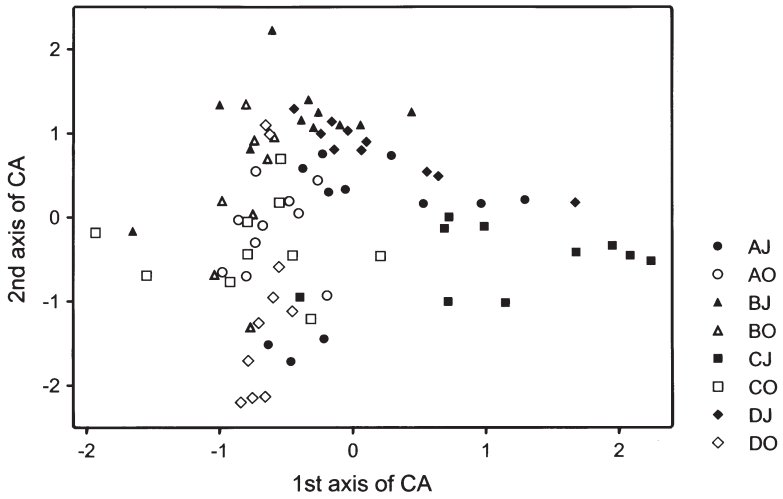


Fig. 5. Correspondence Analysis two axes plane for the monthly samples from different microsites. For microsite codes see Table 1

clearly distinct along the second axis. The effect of altitude seems to concern only the samples from the open microsites. Indeed, the samples from the low altitude stations AO and BO are ordinated at the upper half of the 2nd axis, while those from the high altitude stations CO and DO are ordinated at the lower half.

The ordination results were used for classifying the monthly samples with the fuzzy c-means clustering method. Three clusters were distinguished, representing

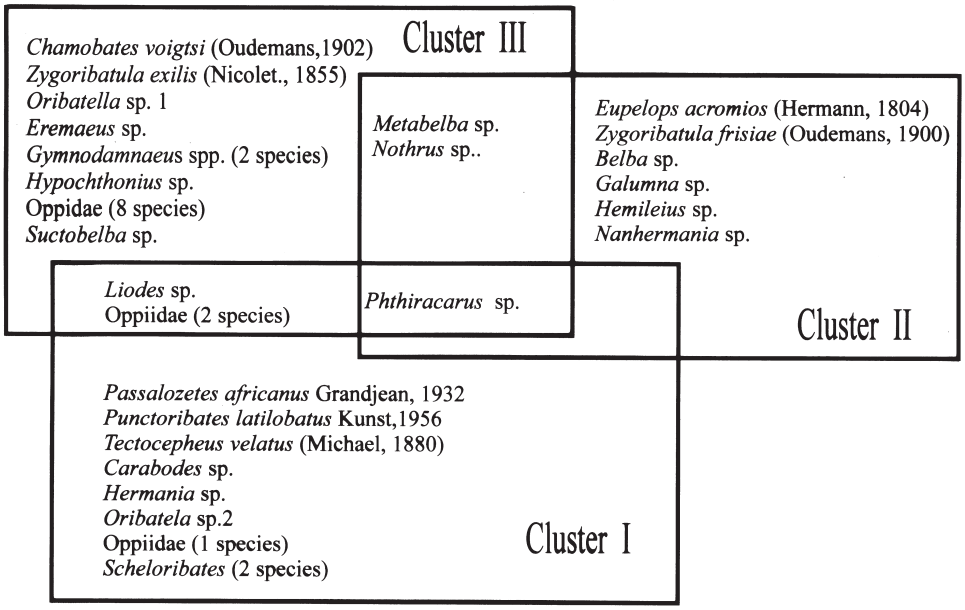


Fig. 6. Oribatid species characterizing the three fuzzy clusters

more or less distinct oribatid species assemblages. A sample is considered member of a cluster, when its membership value to this cluster is above 0.6 in the range [0,1]. In Figure 6, we present the characteristic morphospecies of the three fuzzy clusters. The species characterizing the first cluster (e.g. *Punctoribates latilobatus*, *Scheloribates* spp., *Tectochepheus velatus*, *Passalozetes africanus*) were of intermediate body size, while those of the second (e.g. *Belba* sp., *Eupelops acromios*, *Gymnodamaeus* sp., *Galumna* sp., *Zygoribatula frisiae*) were relatively large sized animals. The third fuzzy cluster consisted of small sized species like *Oppia* spp., *Suctobelba* sp. and *Hypochthonius* sp.

In Figure 7, we distinguish the samples of the three clusters according to their position in relation to the *Juniperus* shrubs (Fig. 7a), the altitude (Fig. 7b) and the month of collection (Fig. 7c). The oribatid community represented by the first cluster showed a clear preference for the open microsites and was present in all stations. It was active during the warm period of the year, showing dominance in spring, a steady decline until autumn and a total absence during winter. The community of the second cluster inhabited both the sheltered and the open microsites, in all stations except C. Although present throughout the year, it was more active during the cold period, dominating the autumn and winter samples. The community represented by the third cluster showed a distinct preference for the sheltered microsites of the deciduous woodland of station C, and did not follow any seasonal pattern.

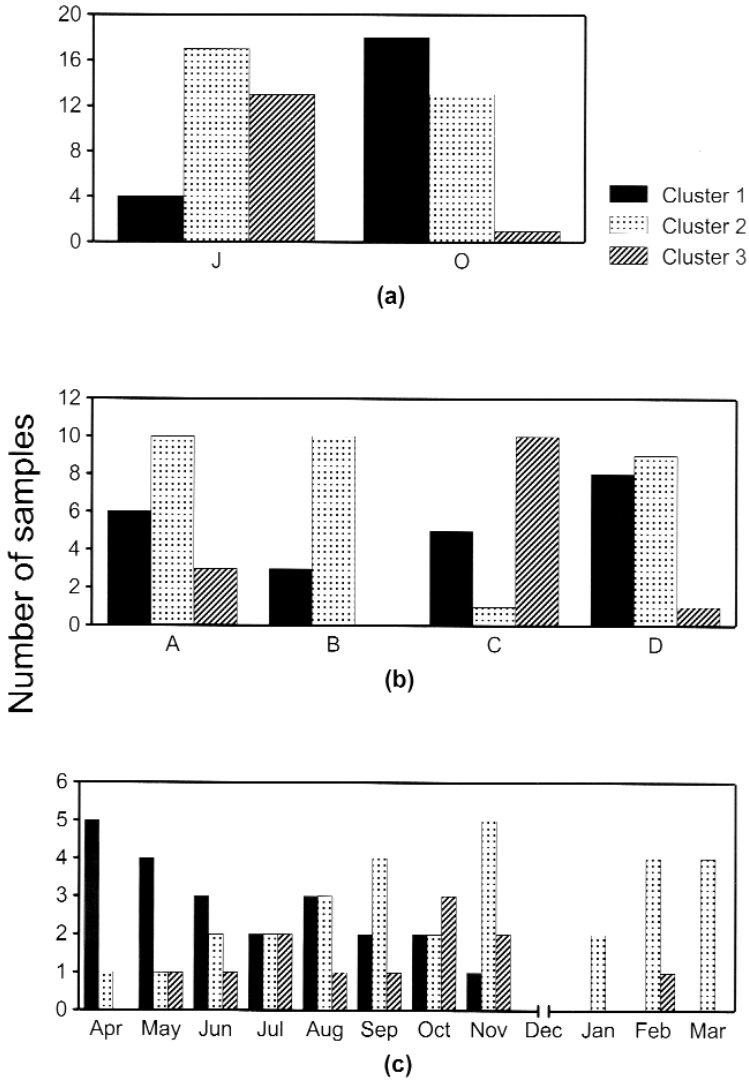


Fig. 7. Fuzzy classification of monthly samples from the different microsites. Distinction of the 3 fuzzy clusters according to (a) shrub coverage, (b) altitudinal station and (c) month of collection

Discussion

The variability of ecological factors in space creates different microhabitats and thus determines the spatial distribution of organisms. In this study we sampled the litter inside the *Juniperus* shrubs and the adjacent grass covered openings, along an elevation gradient, in order to assess spatial distribution patterns of soil microarthropods at two scales: a coarse regional corresponding to the altitudinal gradient, and a fine local one created by the variation in vegetation cover.

Habitat properties affecting the densities of soil fauna at the local scale include the exposure to temperature and moisture fluctuations (Tomlin & Miller 1987) and the amount of available organic material (Usher 1976; Holt 1981; Schenker 1984; Tousignant & Coderre 1992). In this study, both the abundance and the number of oribatid species follow the same trend, i.e. higher values in the sheltered microsites as well as in the C station deciduous woodland. No altitudinal effect is detected in either case. It seems that the higher humidity levels and the smoother temperature fluctuations of the shrubby sites, as well as the accumulated *Juniperus* litter, may buffer the large scale climatic conditions, as Schenker & Block (1986) suggest, and might explain why changes in both abundance and number of species are pronounced at the local scale but not at the regional one. Species poor oribatid mite communities of open grassy sites have also been reported by Tomlin and Miller (1987), Salona & Iturrondobeitia (1993) and Iturrondobeitia et al. (1997). As regards the C station, we should note that in this sampling station the *Juniperus* shrubs dominate the shrub layer of a well stratified woodland, where the overstorey consists of *Carpinus orientalis*. Such formations allow the differentiation of microhabitats for mite populations (Salona & Iturrondobeitia 1993). Lamoncha & Crossley (1998) and Schatz (1998), working with elevation gradients in the Appalachian Mts. and the Galapagos islands respectively, report the forest floors as the richest habitats regarding oribatid species. Thus, although in the work presented here we tried to minimize the effect of local vegetation by sampling similar microsites along the altitudinal gradient, the species recorded in station C might be part of the richer species pool of this area. Walter (1985) who also tried to minimize the vegetation and litter quality effect by sampling oribatids colonizing litterbags placed in coniferous forests at different elevations, found a negative effect of increasing altitude on the number of oribatid species. However, the altitudinal and climatic differences of his sites were much larger than in the present study.

The diversity profiles of the sampling sites showed that inside the shrubs there are few species dominating the oribatid community and many others forming small assemblages, while the species inhabiting the open microsites, although fewer are equally abundant. The coexistence of dominant and rare species, as is the case with the sheltered microsites, indicates habitat heterogeneity (Argyropoulou et al. 1994). It is possible that the accumulated litter under the shrubs provides a structurally more heterogeneous habitat for the oribatid populations. On the other hand, Schenker & Block (1986) state that the homogenous structure of open habitats and the climatic extremes are responsible for the low number of species and low abundance, respectively. The environment of the open sites is hostile for many species, which as Sgardelis and Usher (1994) suggest may be demographically explained in relation to the short period available for population growth.

Further analysis of community structure revealed that while the oribatid communities of the open sites across the elevation gradient appear similar to each other, the

ones inhabiting the *Juniperus* litter display distinct differences, which means that the local scale effect is not equally pronounced at all altitudinal stations, i.e. along the regional scale. Moreover, the consideration of monthly samples revealed also a temporal separation of oribatid niches. More specifically, a distinct oribatid community inhabits the grass-covered openings at all altitudes and is composed of species active during the warm period of the year. A second one exploits both shrubby and grassy sites, mostly during autumn and winter, while a third is present throughout the year almost exclusively inside the shrubs of the deciduous woodland. Anderson (1978b) assumed that while oribatids may frequently share resources over a period of time or in one patch of the habitat mosaic, they are capable of niche differentiation over short time periods if resources become limiting. Our results indicate that in the exposed sites, the strong fluctuations of environmental variables lead to a seasonal succession of communities I and II. A relevant pattern is also noted by Asikidis & Stamou (1991). In the sheltered sites, the changes in community composition are more complicated, since the species of those sites are either capable of inhabiting the open sites as well (community II) or persist throughout the whole year (community III).

To sum up, the two scale effects (i.e. altitude and vegetation cover) are not equally important in shaping the oribatid communities. Altitude per se does not induce any clear pattern of spatial distribution, acting mostly indirectly through the effect on the formation of local vegetation. On the contrary, the temporal or the structural heterogeneity of the habitat or both, operating at the local scale, impose profound changes in oribatid distribution. Oribatids respond to habitat heterogeneity forming separate communities with distinct characteristics.

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