Environmental responses of soil arthropod communities along an altitudinal-climatic gradient of Western Crete in Greece.

Canella Radea and Margarita Arianoutsou*
Department of Ecology and Systematics, Faculty of Biology, University of Athens, 15784 Greece
marianou@biol.uoa.gr

*corresponding author

Keywords: Canonical Correspondence Analysis, Crete, environmental factors, mediterranean shrublands, soil invertebrates, temporal distribution

Abstract

The structure of soil arthropod communities was studied in five sites along an altitudinal-climatic gradient in Western Crete, Greece over a period of one year. The sites located at the higher altitudes had both richer soil arthropod fauna and higher mean annual density of the existing taxa. However, the temporal distribution of overall soil arthropod density followed the same pattern across the sites of the altitudinal gradient. Canonical correspondence analysis applied on the data ordained the sites in relation to the response of soil arthropod communities' structure to several environmental variables. These variables were the presence of a well-formed organic horizon, vegetation cover, amount of precipitation, land management and season. The ability of soil arthropod fauna to "classify" sites with different characteristics was confirmed. It was concluded that soil arthropods, even at ordinal-level, can be used as "indicators" of the responses of mediterranean-climate ecosystems to various environmental variables.

Introduction

The two most distinctive features of mediterranean-climate ecosystems are probably the dominance of sclerophyllous plants in the vegetation and the life of numerous groups of hygrophilous invertebrates deep in the soil (di Castri & Vitali-di Castri 1981). In these ecosystems, soil organic matter and water availability are the two key environmental factors which control the dynamics of soil invertebrate populations (di Castri & Vitali-di Castri 1981). Mediterranean-climate ecosystems have long ago been subjected to anthropogenic influence or even disturbances, such as deforestation, grazing, agriculture and fire. This influence dates back to at least 10000 years, when agricultural civilizations developed over the region (e.g. Le Houerou 1981, Naveh 1998). Many of the practices applied were more or less sustainable, thus resulting to the establishment of a man-maintained dynamic equilibrium (Arianoutsou 2001). However, the combined effects of climatic and human impacts and especially the intensification of above practices started after the Second World War, have led to continuous degradation of Mediterranean regions and to landscape deterioration in Mediterranean basin (Burke & Thornes 1998, Stamou 1998).

Soil arthropod fauna is an ecosystem component that it is quite often used as a research tool for many reasons. First, soil sub-system has a high number of arthropod taxa, usually in high densities (e.g. Chilardov 1977). Arthropods play an important role in organic matter breakdown, hence in nutrient cycling (e.g. Mc Brayer et al. 1977, Tian et al. 1997) and they contribute to the creation and maintenance of a good soil quality (e.g. Schrader et al. 1997, Knoepp et al. 2000). On the other hand, soil arthropod communities have been extensively used as sites 'classifiers' because they respond differently to environmental conditions. For example, Sgardelis & Margaris 1993, Sgardelis et al. 1995, Broza & Izhaki 1997, Mollina et al. 1999, Seymour & Dean 1999, Wardle et al. 1999, Bird et al. 2000 have used soil arthropods in the classification of sites with different land management. Bran-
quart et al. 1995, Ponge et al. 1997 have found that soil arthropods can be used in the classification of forest stands with different productivity and humus type. Eijsackers 1983, Rivers-Moore & Samways 1996 have classified sites disturbed by human activities based on soil arthropods while van Straalen 1998, Kay et al. 1999 and Knoepp et al. 2000 have used soil arthropods as bioindicators of soil quality.

This paper reports on a study that has been undertaken under the framework of an European Project ENV4-CT95-0181, namely 'ERMES II' (Environmental Responses of Mediterranean EcoSystems). An altitudinal gradient located at the west part of Crete was one of the three sites studied across the Mediterranean.

The specific aims of the present work are: i) to investigate which environmental variables can better "explain" the structure of soil invertebrate communities and their temporal patterns in mediterranean-climate localities ii) to ordinate these localities according to the structure of soil communities and their responses to the environmental variables and iii) to evaluate the 'classification' ability of soil invertebrates.

**Study sites**

Three localities were selected (Omalos, Rodopos, Kolympari) along an altitudinal-climatic gradient of Western Crete ranging from sub-humid conditions at Omalos location to semi-arid at the lowest site of Kolympari (Fig. 1, Fig. 2).

![Fig. 1. Locations of the sites studied along the altitudinal-climatic gradient in Western Crete.](image)

![Fig. 2. Ombrothermic diagrams of the sites studied along the altitudinal-climatic gradient in Western Crete.](image)

In Omalos locality two sampling sites were established: one in the foothills (Omalos low=OMl) and the other at the middle (Omalos high=OMh) of the relevant slope. Rodopos locality was also sampled at two distinct sites, one burned a couple of years ago and one unburned. Both sites had the same slope. Kolympari locality was homogeneous and flat, so it was treated as one site. This site was also been
burned a couple of years ago. All localities were situated on south-facing slopes on limestone substrate and they were grazed by sheep and goats.

At the Omalos locality, which is the upper limit of the altitudinal range studied, the vegetation is a well-developed maquis with high shrubs and subshrubs. The evergreen sclerophyllous tall shrub Quercus coccifera and the seasonal dimorphic subshrub Phlomis cretica dominate in OMh. OMI is dominated by a tall deciduous shrub that is Acer sempervirens and by Phlomis cretica.

In Rodopos, two sites were established: one burned and one unburned. Rodopos has a different type of vegetation. The plant community is phrygana with a few scattered evergreen sclerophyllous tall shrubs of Quercus coccifera (burned site) and Pistacia lentiscus (unburned site). Sarcopoterium spinosum, a seasonal dimorphic subshrub, dominates in both sites.

Kolympari site is of phryganic type too. The dominant plant species is the dwarf shrub Sarcopoterium spinosum and only a few scattered individuals of evergreen sclerophyllous tall shrubs Pistacia lentiscus and Olea europaea occur. The characteristics of the sites are indicated in Table 1. For vegetation cover three classes were distinguished, high, medium and low corresponding to a cover over 60%, between 30-60% and less than 30% respectively (Orr, 1970). At the Omalos’ sites, the organic horizon has a patchy distribution. A rather thick and loose organic horizon (L and F+H layers present) is formed under the shrub canopy while among the shrubs a thin organic horizon exists (L-layer present) formed by the litter falling from the tall shrubs. At the unburned site of Rodopos a thin organic horizon (Land F+H layers present) occurs homogeneously throughout the area due to the high vegetation cover characterising this site. In the recently burned sites of Rodopos and Kolympari the organic horizon had not yet being formed since its consumption by fire, a vestigial L-layer being dispersed scarcely.

Methods

The study of the structure of soil arthropod communities along the altitudinal-climatic gradient was realised by collecting sample units of the soil organic horizon with a sharp edge cylinder of 100 cm². Fieldwork was performed between June 1996 and June 1997. During this period four field campaigns were conducted covering the overall seasonal variation: June, October, February and May. On each sampling occasion five randomly distributed samples covering the whole range of the site were taken from each of the five sites. Each sample consisted of the organic layers and the first 2 cm of the underlying inorganic soil horizon. Every sample unit was sealed in a plastic bag and was transported to the laboratory. The arthropods were extracted from the samples by means of a Berlese-Tullgren apparatus. The specimens were collected in 75% ethanol solution with 5% glycerine, identified to the level of order and counted under a stereomicroscope.

Several environmental variables are known to define soil community structure as well as its temporal pattern in mediterranean-climate ecosystems (di Castri 1973, di Castri & Vitali-di Castri 1981, Ra-dea 1989, Sgardelis et al. 1995, David et al. 1999 among others). The environmental variables selected in the present study were altitude, precipitation, season, presence of organic horizon, fire (an indication of land management) and vegetation cover. The values for the latter variable were obtained from Arianoutsou & Kazanis (unpublished data). Unfortunately reliable data about grazing intensity in the five localities are not available and, thus, fire is the only land management type tested.

Table 1. Characteristics of the sites studied along the altitudinal-climatic gradient in Western Crete.

<table>
<thead>
<tr>
<th>Characteristics</th>
<th>OMh</th>
<th>OMI</th>
<th>ROu</th>
<th>ROb</th>
<th>KO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m)</td>
<td>1100</td>
<td>1070</td>
<td>300</td>
<td>300</td>
<td>50</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>39</td>
<td>27</td>
<td>6</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Aspect</td>
<td>S210</td>
<td>S210</td>
<td>$S185$</td>
<td>$S185$</td>
<td>S200</td>
</tr>
<tr>
<td>Lithology</td>
<td>Limestones (Triassic)</td>
<td>Limestones (Triassic)</td>
<td>Limestones (Triassic)</td>
<td>Limestones (Triassic)</td>
<td>Limestones (Triassic)</td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>1570</td>
<td>1570</td>
<td>950</td>
<td>950</td>
<td>549</td>
</tr>
<tr>
<td>Vegetation cover (%)</td>
<td>Medium</td>
<td>Medium</td>
<td>High</td>
<td>Medium</td>
<td>Medium</td>
</tr>
<tr>
<td>Dominant plants in cover</td>
<td>Quercus coccifera</td>
<td>Acer sempervirens</td>
<td>Sarcopoterium spinosum</td>
<td>Sarcopoterium spinosum</td>
<td>Sarcopoterium spinosum</td>
</tr>
<tr>
<td>Organic horizon's thickness (cm)</td>
<td>2.7–2.3</td>
<td>2.3–2.2</td>
<td>1.9–1.1</td>
<td>&lt;0.5</td>
<td>&lt;0.5</td>
</tr>
</tbody>
</table>
The statistical program CANOCO\textsuperscript{TM} 4.0 for Windows was used for the ordination of sites. The abundance data of taxa were transformed by taking logarithms to down-weighted high abundance. Values for the environmental variables are either in ordinal or in nominal scale.

**Results**

The soil arthropod taxa collected at each site, their code name and the mean annual density of their populations are shown in Table 2. A comparison between the sites studied suggests the following sequences of decreasing richness of taxa and average densities OMh\textgreater OMl \textgreater ROu \textgreater ROb=KO. The structure of arthropod communities differed at the five sites, since the percentages of the various xerophilous taxa of soil arthropods, namely Araneae, Polyxenida, Thysanura, Psocoptera, Coleoptera (di Castri 1973) were 4.2\%, 4.8\%, 5.7\%, 11.8\% and 10.3\% in OMh, OMl, ROu, ROb and KO respectively.

The temporal distribution of soil arthropod taxa in total followed the same pattern at all sites of the altitudinal-climatic gradient. The maximum of density was observed during the wet period of the year and the minimum during the warm and dry period (Fig. 2).

**Canonical correspondence analysis**

Canonical Correspondence Analysis (CCA) was successfully performed using the data concerning the abundance of soil arthropods and the environmental variables mentioned above (Table 3).

The results of CCA revealed that a high percentage of variance of the taxa data (54.5\%) can be explained by the four canonical axes and, moreover, a remarkable percentage of the explainable variance (95.3\%) can be accounted for by the environmental variables chosen.

The ordination of groups of sites and of the arthropod taxa is depicted on the plan of the first two most significant axes of CCA (Fig 4a, 4b).

Canonical coefficients (Table 4) are sufficient for interpreting canonical axes since there were no high correlation among the environmental variables (Table 5) (Ter Braak 1986).

The statistical significance of the relation between the taxa and the whole set of environmental variables

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Code name</th>
<th>OMh</th>
<th>OMI</th>
<th>ROu</th>
<th>ROb</th>
<th>KO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pseudoscorpionida</td>
<td>Pseud</td>
<td>565±20</td>
<td>1483±50</td>
<td>1566±26</td>
<td>0</td>
<td>2±1</td>
</tr>
<tr>
<td>Araneae</td>
<td>Aran</td>
<td>400±12</td>
<td>1130±216.1</td>
<td>301±21</td>
<td>5±1</td>
<td>6±2</td>
</tr>
<tr>
<td>Acarina</td>
<td>Acar</td>
<td>55060±929</td>
<td>45620±6758</td>
<td>22793±352</td>
<td>55±32</td>
<td>39±4</td>
</tr>
<tr>
<td>Polyxenida</td>
<td>Plx</td>
<td>2825±70</td>
<td>636±185</td>
<td>724±27</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Iulida</td>
<td>Iul</td>
<td>282±26</td>
<td>0</td>
<td>424±25</td>
<td>0</td>
<td>1±1</td>
</tr>
<tr>
<td>Craspedosomida</td>
<td>Crsp</td>
<td>71±20</td>
<td>71±20</td>
<td>88±8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lithobiomorpha</td>
<td>Lith</td>
<td>424±18</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1±1</td>
</tr>
<tr>
<td>Geophilomorpha</td>
<td>Geo</td>
<td>212±8</td>
<td>636±266</td>
<td>177±7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Isopoda</td>
<td>Isop</td>
<td>1695±60</td>
<td>3178±1695</td>
<td>229±12</td>
<td>3±1</td>
<td>8±2</td>
</tr>
<tr>
<td>Collembola</td>
<td>Coll</td>
<td>31199±1056</td>
<td>15706±7314</td>
<td>11193±257</td>
<td>15±2</td>
<td>19±10</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>Hem</td>
<td>442±182</td>
<td>5508±1723</td>
<td>71±5</td>
<td>0</td>
<td>2±2</td>
</tr>
<tr>
<td>Thysanoptera</td>
<td>Thys</td>
<td>565±15</td>
<td>989±385</td>
<td>141±7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pscoptera</td>
<td>Psoc</td>
<td>400±8</td>
<td>918±50</td>
<td>1377±312</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Cole</td>
<td>989±34</td>
<td>1483±347</td>
<td>177±8</td>
<td>2±2</td>
<td>0</td>
</tr>
<tr>
<td>Emphiptera</td>
<td>Emb</td>
<td>0</td>
<td>424±69</td>
<td>688±18</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Diptera</td>
<td>Dipt</td>
<td>471±20</td>
<td>706±100</td>
<td>247±8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Symphylla</td>
<td>Sym</td>
<td>282±18</td>
<td>353±117</td>
<td>636±22</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Diplura</td>
<td>Dipl</td>
<td>212±18</td>
<td>1130±388</td>
<td>141±10</td>
<td>0</td>
<td>2±2</td>
</tr>
<tr>
<td>Protura</td>
<td>Prot</td>
<td>565±27</td>
<td>141±68.8</td>
<td>71±5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pauropoda</td>
<td>Pau</td>
<td>706±59</td>
<td>1059±423</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Thysanura</td>
<td>Thysa</td>
<td>612±18</td>
<td>424±128</td>
<td>89±7</td>
<td>3±1</td>
<td>3±1</td>
</tr>
<tr>
<td>Dictyoptera</td>
<td>Dict</td>
<td>424±30</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Coleoptera larvae</td>
<td>L. Cole</td>
<td>1059±22</td>
<td>1907±289</td>
<td>547±14</td>
<td>0</td>
<td>1±1</td>
</tr>
<tr>
<td>Diptera larvae</td>
<td>L. Dipt</td>
<td>282±12</td>
<td>10169±943</td>
<td>4308±103</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lepidoptera larvae</td>
<td>L. Lep.</td>
<td>636±21</td>
<td>777±312</td>
<td>406±8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total density</td>
<td></td>
<td>104361</td>
<td>94448</td>
<td>46394</td>
<td>83</td>
<td>82</td>
</tr>
</tbody>
</table>
This test showed that the most significant relations were the ones with season \((p=0.0005)\), organic horizon presence \((p=0.0010)\), vegetation cover \((p=0.0025)\), precipitation \((p=0.0235)\) and fire event \((p=0.0310)\).

CCA-biplot ordination diagrams of arthropod taxa and sites (axis 1 and 2, axis 1 and 3) are shown in Fig. 4.

The results of CCA showed that axis 1 accounted for 25.5% of the total variance among taxa and was correlated with the season \((t=-10.12)\). Axis 1 was a gradient from the wet to the dry period and separated clearly the samples collected during the wet period of the year (October, February) from those of the dry period (June, May). This fact indicates that at all sites the structure of the arthropod community in the wet period differed completely from that in the dry period of the year. This axis separated also the hygrophilous-mesophilous arthropod taxa (such as dipteran larvae, Polydesmida, Craspedosomida, Iulida, Isopoda and Pseudoscorpionida), which showed the peak of their density during the wet period, from the xerophilous-mesophilous taxa (such as Pscoptera, Thysanura, Araneae and Hemiptera), which exhibited their highest density during the dry period of the year.

Canonical axis 2 accounted for 15.4% of the total variance and was correlated with the organic horizon \((t=-12.80)\), fire \((t=-7.47)\), precipitation \((t=-6.72)\) and vegetation cover \((t=4.36)\). This axis showed that the samples taken during the wet period from the burned phrygana sites (organic horizon absent) were quite similar to those collected during the dry period from the unburned maquis site (presence of a thick organic horizon). This axis also separated two sites, that is OMh and ROu, from each other. Both sites were characterised by the presence of a well-formed organic horizon but the first had the thickest organic horizon and the latter the thinnest one. Axis 2 separated two groups of arthropod taxa; the first consisted mainly of Hemiptera, Dictyoptera, Pauropoda, Polydesmida, Polyxenida, Isopoda and the second of Iulida, Diptera larvae, Pscoptera, Embioptera, Lithobiomorpha and Pseudoscorpionida.

Axes 3 and 4 were less significant and they accounted for 7.1% and 6.5% of the total variance respectively. Axis 3 was correlated with vegetation cover \((t=-5.90)\), presence of an organic horizon \((t=3.85)\) and fire \((t=2.65)\) and axis 4 was correlated with precipitation \((t=-10.80)\), vegetation cover \((t=-4.70)\), season of the year \((t=3.72)\) and fire event \((t=2.49)\).

Taking into account the above data and the ordination diagram in Fig. 3, it is obvious that the samples of ROu constitute a rather homogeneous group clearly distinct from the others with respect to organic horizon, precipitation, vegetation cover and fire.

**Discussion**

The density of soil arthropod recorded in the maquis (OMh, OMl) and the unburned phrygana (ROu) sites are much higher than those reported by Sgardelis et al. (1981) for other unburned phrygana sites of Greece \((37620 \text{ ind/m}^2)\). However, the soil arthropod fauna of phrygana in ROb and KO is an impoverished one. Soil arthropod density values recorded at these sites are considerably lower than tho-

---

**Table 3.** Results of Canonical Correspondence Analysis

<table>
<thead>
<tr>
<th>Axis variable</th>
<th>Axis 1</th>
<th>Axis 2</th>
<th>Axis 3</th>
<th>Axis 4</th>
<th>Total inertia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalues</td>
<td>0.207</td>
<td>0.125</td>
<td>0.057</td>
<td>0.052</td>
<td>0.811</td>
</tr>
<tr>
<td>Taxa-environment</td>
<td>0.944</td>
<td>0.973</td>
<td>0.877</td>
<td>0.960</td>
<td></td>
</tr>
<tr>
<td>Correlation of taxa data</td>
<td>25.5</td>
<td>40.9</td>
<td>48.0</td>
<td>84.0</td>
<td>95.3</td>
</tr>
<tr>
<td>Correlation of taxa-env</td>
<td>44.7</td>
<td>71.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum of all constrained</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.811</td>
</tr>
<tr>
<td>Sum of all canonical</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.463</td>
</tr>
</tbody>
</table>
se reported by Sgardelis & Margaris (1993) and Sgardelis et al. (1995) for other burned phrygana of central Greece (10000 ind/m²).

The results of CCA denote that the spatial distribution of soil arthropod taxa is clearly affected by the amount of precipitation, the vegetation cover, the presence of a well-formed organic horizon and the fire event. It is well known that climatic factors influence soil fauna either directly by affecting the soil microclimate and/or indirectly through the vegetation type they favor (di Castri & Vitali-di Castri 1981). Vegetation type controls soil fauna through the quantity and quality of litter and the physical effects of vegetation cover on soil microclimate and surface protection (Swift & Anderson 1994). Noteworthy is the fact that in Mediterranean-type ecosystems the amount of soil organic matter is rather low (di Castri 1973) and, therefore, its role in the structure of soil fauna is of great importance.

At the localities of Rodopos and Kolympari, where the precipitation is much lower than that in Omalos, the dominant plant species is Sarcopoterium spinosum i.e. a low seasonal dimorphic shrub. Both summer and winter leaves of this species are particularly small (Arianoutsou-Faraggitaki & Diamantopoulos 1985) and remain intact in the litter layer for only a short time (Fousseki & Margaris 1981). Thus, the organic horizon formed is very thin although the vegetation cover is not low. Omalos sites are dominated either by an evergreen sclerophyllous tall shrub (Quercus coccifera in OMh) or by a deciduous sclerophyllous tall shrub (Acer sempervirens in OMI). Leaves of both species are larger than those of phryganic ones and are shed in large amounts (Arianoutson 1989 and personal observation). Their relatively low decomposition rate (Arianoutsou 1993) leads to the formation of a thicker organic horizon. Therefore, the high number of arthropod taxa and individuals at Omalos’ sites is mainly attributed to the favourable characteristics of the organic horizon as well as to high precipitation and vegetation cover.

Canonical Correspondence Analysis ordnates the arthropod taxa into two main groups. The first group includes taxa, which are greatly depended on the thickness of organic horizon. These are Pauropoda, Polydesmida, Polyxenida, Isopoda, Geophilomorpha (Wallwork 1970, Petersen & Luxton 1982) which prefer deep organic layers. The second group consists of those, which are able to migrate upwards at least during the wet period; these are Julida, Diptera larvae, Embiotreta, Lithohiomorpha and Pseudoscorpionida (Wallwork 1970, Radea 1989, Marmari 1991).

Fire is another surcharged factor for the ROB and KO sites. Fire alters the quantitative and qualitative composition of soil arthropod community (Sgardelis & Margaris 1993, Sgardelis et al. 1995, Broza & Izhaki 1997). In the burned sites the combination of low vegetation cover and low precipitation results to a poor composition of the arthropod fauna. Xerophilous-mesophilous arthropods, which are able to persist under the unfavourable conditions in the soil sub-system, are highly represented. Although fire is of comparatively lower significance (Monte

---

**Table 4. Canonical coefficients and intraset correlation coefficients for the first four axes of canonical correspondence analysis**

<table>
<thead>
<tr>
<th>Axis variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>-0.9833</td>
<td>0.0728</td>
<td>-0.1251</td>
<td>0.3027</td>
</tr>
<tr>
<td>Orghor</td>
<td>-0.1155</td>
<td>-1.0825</td>
<td>0.7462</td>
<td>-0.1071</td>
</tr>
<tr>
<td>Vegcover</td>
<td>-0.1915</td>
<td>0.2944</td>
<td>0.9145</td>
<td>0.3883</td>
</tr>
<tr>
<td>Precipit</td>
<td>0.0219</td>
<td>-0.4683</td>
<td>-0.2913</td>
<td>0.9194</td>
</tr>
<tr>
<td>Fire</td>
<td>-0.0485</td>
<td>-0.5916</td>
<td>0.4825</td>
<td>0.2412</td>
</tr>
</tbody>
</table>

---

**Table 5. Mutual correlation of environmental variables used in canonical correspondence analysis**

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Season</th>
<th>Orghor</th>
<th>Vegcover</th>
<th>Precipit</th>
<th>Fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>1.0000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orghor</td>
<td>0.0407</td>
<td>1.0000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegcover</td>
<td>0.0406</td>
<td>-0.2520</td>
<td>1.0000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precipit</td>
<td>0.2748</td>
<td>-0.2893</td>
<td>0.1209</td>
<td>1.0000</td>
<td></td>
</tr>
<tr>
<td>Fire</td>
<td>0.0402</td>
<td>-0.5618</td>
<td>-0.0271</td>
<td>0.1031</td>
<td>1.0000</td>
</tr>
</tbody>
</table>
Carlo permutation test), there is a notable differentiation in the structure of the arthropod community between the burned phrygana and the unburned sites. This difference becomes more accentuated when burned phrygana sites are compared to unburned maquis sites. Samples collected during the favourable, wet period in the first sites have similar composition with those collected during the unfavourable, dry period in the second group of sites. It is remarkable that all samples from the unburned phrygana at Rodopos formed a distinct and isolated group (Fig 4A, 4C). This fact reflects the response of the arthropod fauna to the characteristics of this specific site, which are different from those of all the other sites. It seems that the arthropod community in the unburned phrygana consists of taxa adapted to the peculiarities of this site and that its structure remains rather stable all year round. On

![Graphs](image-url)

**Fig. 4.** Canonical correspondence analysis based on arthropod density found in the five riles studied along the altitudinal-climatic gradient of Western Crete. **A.** Biplot ordination of study sites in the space of Axes 1 and 2. **B:** idem for arthropod taxa. **C:** Biplot ordination of study sites in the space of Axes 1 and 3. **D:** idem for arthropod taxa. **Axis 1** is horizontal. **Axes 2 and 3** are verticals.
the contrary, the structure of the arthropod community in the unburned maquis and in the burned phrygana seems to change during the year. This is probably due to the vertical migration of various soil arthropod taxa in the maquis localities and to the unstable and unfavourable conditions that fire has caused in the burned ones.

Temporal distribution of taxa depends on the season of the year in all study sites. A peak is shown in arthropod taxa in the maquis localities and to the contrary, the structure of the arthropod community in the unburned maquis and in the burned phrygana seems to change during the year. This is probably due to the vertical migration of various soil arthropod taxa in the maquis localities and to the unstable and unfavourable conditions that fire has caused in the burned ones.

In summary, a clear ordination of the five sites along the altitudinal-climatic gradient of West Crete was detected and it is due to the structure of soil arthropod community. The ability of soil arthropods to "classify" sites with different environmental characteristics is thus confirmed. Hence, soil arthropods, even at ordinal level, could be used as an "indicator" of the environmental responses of mediterranean-climate ecosystems.

Acknowledgements

The European Union, DG XII, Environment and Climate Programme, under the project ERMES II, ENV4-CT95-0181, financially supported the work.

References


In summary, a clear ordination of the five sites along the altitudinal-climatic gradient of West Crete was detected and it is due to the structure of soil arthropod community. The ability of soil arthropods to "classify" sites with different environmental characteristics is thus confirmed. Hence, soil arthropods, even at ordinal level, could be used as an "indicator" of the environmental responses of mediterranean-climate ecosystems.


