

Epidaphic Coleoptera in the Dadia forest reserve (Thrace, Greece) : the effect of human activities on community organization patterns

Maria D. Argyropoulou¹, George Karris¹, Efi M. Papatheodorou² and George P. Stamou²

¹ Dept. of Zoology, School of Biology, UPB 134, Aristotle University, GR-54124 Thessaloniki, Greece

² Dept. of Ecology, School of Biology, UPB 119, Aristotle University, GR-54124 Thessaloniki, Greece

Corresponding author : M. D. Argyropoulou, e-mail : margyrop@bio.auth.gr

ABSTRACT. In this work we described and compared the community organization patterns of Coleoptera in various sites of the Dadia forest reserve, including different types of vegetation and management practices (grazing, cultivation, afforestation). Sampling was carried out every two months for a year, by means of pitfall traps. For studying diversity and community structure, we used Renyi's parametric index of diversity and fitted the geometric series model on rank/abundance data. In order to study the changes of species composition, we used the Indicator Value method (IndVal), after a tree clustering of our sampling sites.

According to our results, although the three management practices increased the diversity of epiedaphic Coleoptera, their effects on the community organization patterns were different. Grazing did not affect the species composition of the communities but altered the community structure. The communities in the ungrazed forests were over-dominated by one species, while those of the grazed sites were hierarchically structured. On the other hand, the main effect of cultivation on the coleopteran communities was a profound change in species composition. The cultivated site was dominated by characteristic species that were almost absent from all other sites. Afforestation caused intermediate changes in both community structure and composition.

Finally, although certain species of Coleoptera seemed to be good indices for assessing human impacts on natural environment, the study of changes in the community organization patterns is even more appropriate.

KEY WORDS : Diversity, community structure, indicator species, grazing, cultivation, afforestation.

INTRODUCTION

Different land use and management practices affect the variability of ecological factors in space and consequently the habitat heterogeneity, which is reflected in the communities of soil arthropods. Due to high turnover and growth rates of most species, these animals serve as probes that quickly respond to environmental change (MATTONI et al., 2000). Thus, the use of soil arthropods in monitoring for purposes of conservation biology, although limited until the beginning of the last decade, is continuously increasing.

Many bioindication studies aiming at habitat evaluation and monitoring have been based on the coleopteran fauna, focusing either on certain species or families or even on the whole order (e.g. BOHAC, 1999 ; HUMPHREY et al., 1999 ; MOLINA et al., 1999 ; MAGURA et al., 2000a ; BAUR et al., 2002). In many of these studies, the researchers have tried to assess the effect of human practices, such as grazing (GARDNER et al., 1997 ; PETIT & USHER, 1998), farming activities (KROOSS & SCHAEFER, 1998 ; KROMP, 1999 ; VARCHOLA & DUNN, 1999) and forestry practices (INGS & HARTLEY, 1999 ; MAGURA et al., 2001, 2002) on the coleopteran communities.

In the work we present here, we have tried to describe and compare the community organization patterns of epiedaphic Coleoptera at various sites of the Dadia forest

reserve, which differ regarding vegetation and human activities. The Dadia forest is near the Greek-Turkish border. It is famous for the endangered and/or vulnerable populations of birds of prey, and it is under protection since 1980. Our work was part of a wider monitoring project of the protected area, which was funded by WWF-Hellas, and where several research teams worked on different animal groups as well as on vegetation. Our interest was focused on identifying the importance of three management practices, namely grazing, cultivation and afforestation, in shaping the coleopteran species assemblages. More specifically, we compared the effects of these practices on diversity, community structure and species composition of surface dwelling beetles.

MATERIAL AND METHODS

Study sites and sampling

Ten sites were sampled, including different types of vegetation and management practices (Table 1). Some of these sites were adjacent to each other, forming distinct gradients according to the management practice to which they are subject. For example, the natural pine forest, the grazed pine forest and the overgrazed meadow constituted a gradient of grazing pressure (PINE→gPINE→MEAD). The same holds for the ungrazed and the adjacent grazed area of the mixed oak forest (MOAK→gMOAK).

Another grazed site was a typical mediterranean maquis (MAQ) with a variety of shrub species, which is used as pastureland. Another case was a natural oak-pine forest, an adjacent cultivated field, and a natural hedgerow that is connected to the forest and borders the field (OAK-

P→HEDG→CULT). And lastly, we compared a pine afforestation (AFF) with the natural pine forest, in order to explore the effect of this management practice on the coleopteran community.

TABLE 1
Characteristics of the ten sampling sites within the Dadia protected area.

Site	Code	Habitat characteristics	Management practice
1 Pine forest	PINE	Ungrazed dense mature forest of <i>Pinus brutia</i>	
2 Grazed pine forest	gPINE	Sparse <i>P. brutia</i> trees and grass-covered areas.	grazing
3 Overgrazed meadow	MEAD	Overgrazed grass-covered meadow with microhabitats of bare soil	
4 Mixed oak forest	MOAK	Ungrazed mature forest of <i>Quercus sp.</i> and <i>Carpinus orientalis</i> .	
5 Grazed mixed oak forest	gMOAK	Sparse trees of <i>Quercus sp.</i> , <i>Carpinus orientalis</i> , <i>Fraxinus ornus</i> , <i>Cornus mas</i> , <i>Acer sp.</i> and open grass-covered areas	grazing
6 Mediterranean shrubland	MAQ	Typical mediterranean maquis with <i>Phillyrea latifolia</i> , <i>Juniperus oxycedrus</i> , <i>Erica arborea</i> , <i>Cistus sp.</i> and grass-covered areas	grazing
7 Mixed oak-pine forest	OAKP	Ungrazed mature forest of <i>Pinus brutia</i> and <i>Quercus frainetto</i>	
8 Natural hedgerow	HEDG	The species composition includes <i>Ulmus sp.</i> , <i>Clematis sp.</i> , <i>Rubus spp.</i> , <i>Rosa sp.</i> and <i>Prunus spinosa</i> .	cultivation
9 Cultivated field	CULT	Non-irrigated organic wheat cultivation	
10 Afforestation	AFF	<i>P. brutia</i> afforestation.	afforestation

Sampling was carried out by means of unbaited pitfall traps (diameter 5.4 cm, height 15 cm), every two months for one year. The traps contained 10% ethylene glycol as a killing-preserving solution. We used five traps per site (5x10=50 traps in total), which remained in the field for seven days on each sampling occasion. Samples from the whole experimental year were used for data analysis. All specimens were identified to morphospecies, while for further identification of Carabidae, Staphylinidae and Cerambycidae, expert assistance was offered by the National Museum of Natural History of Bulgaria.

Data Analysis

For assessing the diversity of coleopteran communities in the different sites, we used the method of diversity ordering proposed by RENYI (1961). Renyi's parametric index of order a shows varying sensitivity to the rare and abundant species of a community, as the scale parameter a changes (RICOTTA, 2000). It provides a profile of the most widely used diversity indices. For $a=0$, the index equals \log species number, for $a=1$, it equals Shannon's index, for $a=2$, it equals Simpson's index. For a tending to infinite, the index is most sensitive to the abundant species. Thus, when 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 may be ordered differently by different diversity indices. For calculations we used DivOrd (TOTHMERESZ, 1995).

For further insight into the community structure, we estimated the environmental constant from the rank/abundance plots, as proposed by MAY (1975) and MOTOMURA

(1932). In a geometric series, the abundance of species ranked from most to least abundant is :

$$n_i = N k (1-k)^{i-1} [1-(1-k)^s]^{-1}$$

where n_i = number of individuals of the i th species, N = total number of individuals, s = total number of species and k = environmental constant.

In order to study the changes of species composition at the different sites, we used the IndVal (Indicator Value) method of DUFRENE & LEGENDRE (1997). This method assigns indicator (characteristic) species to a site or a group of sites, on the basis of species relative abundance and relative frequency of occurrence in the various groups of samples. The approach requires a former classification of sample units. We obtained a typology based on a tree clustering of our sampling sites (linkage rule : unweighted pair-group centroid, distance measure : 1-Pearson r). The statistical significance of the species indicator values was also evaluated by the IndVal program by means of a randomization procedure.

RESULTS

Diversity

In Fig. 1a, we present the diversity profiles of the sites that differ due to grazing. In the case of the natural mixed oak forest and the grazed one, we can see that the diversity of the coleopteran community is much higher in the grazed forest than in the natural one. The difference of the two curves falls mainly in the range of high values of the scale parameter. This means that the difference is mostly due to the presence of abundant species in the grazed site, rather than to the higher number of species. The same

holds in the case of the natural and the grazed pine forest. In comparison with these two sites, the overgrazed meadow exhibited intermediate diversity, although the

number of species was higher. As regards the mediterranean pasture land, it exhibited the highest diversity of all sites.

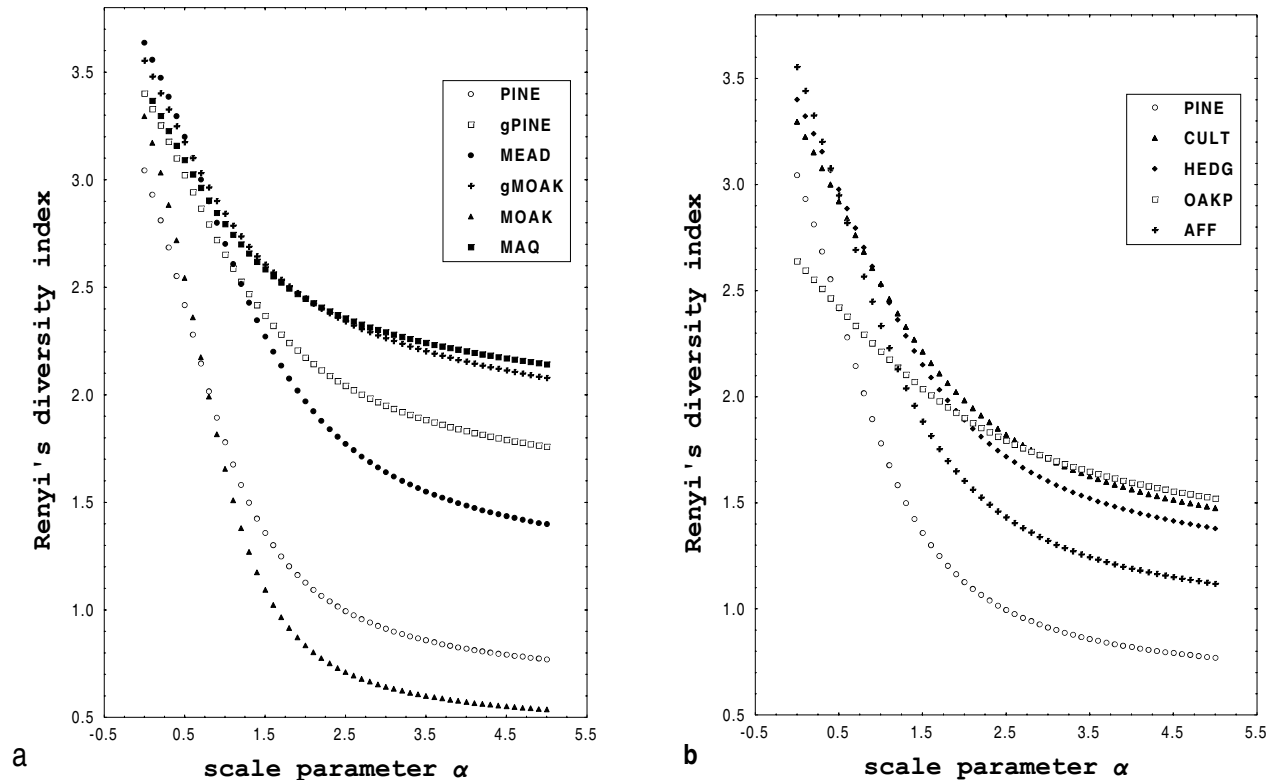


Fig. 1. – Diversity profiles of coleopteran communities (a) in PINE, gPINE, MEAD, MOAK, gMOAK, MAQ and (b) in OAKP, HEDG, CULT, AFF, PINE. PINE was also included in (b) for comparative purposes. For site codes see Table 1.

In Fig. 1b, we present the diversity profiles of the sites that differ due to the two other management practices, i.e. cultivation and afforestation. The diversity profiles of the coleopteran communities in the natural forest, the hedge-row and the cultivated field intersect, which means that the communities may be ordered differently by different diversity indices. What is obvious here is that the natural forest had the lowest diversity, and more specifically the lowest number of species, since the difference of the curves falls in the range of low values of the scale parameter. Moreover, the differences in diversity due to cultivation were not as pronounced as the ones that were caused by grazing.

As regards afforestation, the third management practice, its effect on diversity was intermediate, compared to the effects of grazing and cultivation. The afforested site was more diverse than the natural pine forest, both regarding the species number and the equitability, since the two diversity curves differ equally through the whole range of the scale parameter.

Community structure

In Fig. 2, we present the rank/abundance plots for all sites together with the values of the environmental constant (k). Comparing the natural with the grazed oak for-

est, we can see that in the natural forest one species over-dominated the community and almost all the others were represented by very low numbers. This is the reason for the high value of the environmental constant. At the grazed site, dominance was shared by several species, and the value of the constant was very low. The same changes in community structure may also be observed in the case of the natural and the grazed pine forest, i.e. an over-dominance of a single species at the natural site and a more hierarchical community structure at the grazed site. The hierarchical community structure was most obvious in the mediterranean pastureland, which exhibited the lower value of the environmental constant.

These changes of community structure cannot be observed in the case of the sites that differ due to cultivation. The values of the environmental constant were almost the same for the three sites, which means that this management practice does not induce pronounced changes in community structure as is the case with grazing.

As regards afforestation, it is obvious from the rank/abundance plots and the values of the environmental constant, that the changes in community structure were once again intermediate, compared with those induced by grazing and cultivation.

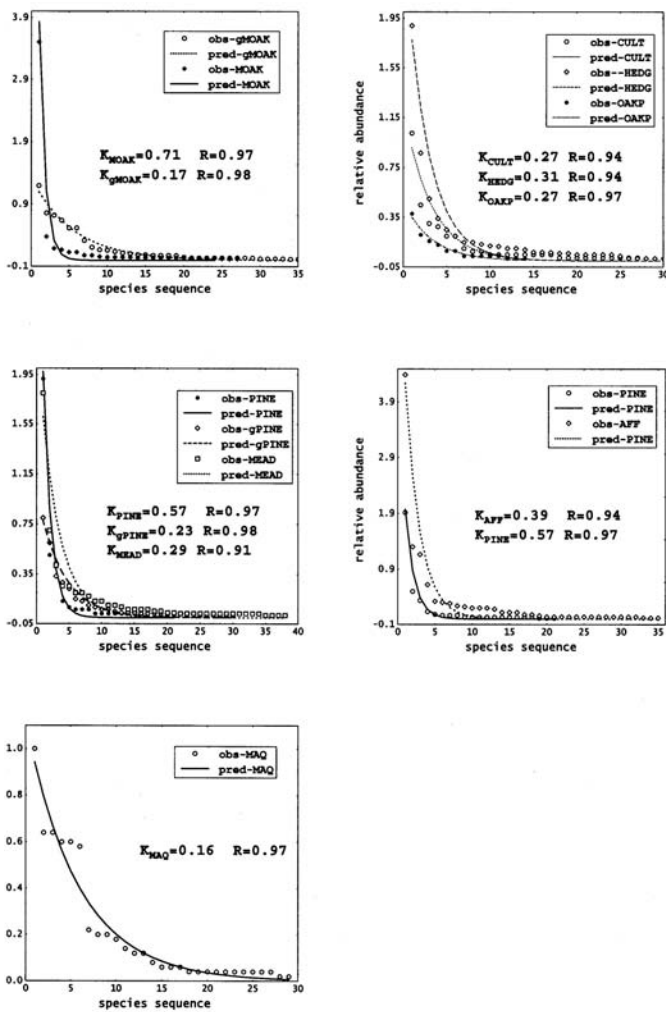


Fig. 2. – The geometric series model fitted on rank/abundance data from all sampling sites. Species are ordered from the most to the least abundant. The environmental constant (k) and the goodness of fit (R) are also noted. For site codes see Table 1.

Species composition

In order to explore changes in species composition due to the three management practices, we used the IndVal method after a tree clustering of our sites. Species recorded only on one sampling occasion were not taken into account in this analysis and thus the whole number of species recorded in this study was reduced to 34. The results are presented in Fig. 3 and Table 2. In the dendrogram of Fig. 3, we can see that the natural sites are grouped together; the same happens with most of the grazed sites, while the cultivated field and secondly the pine afforestation are separated from all the others. These two sites have the greatest number of characteristic species. We must note here that the characteristic species of the cultivated field were also the dominant ones at this site. As regards the pine afforestation, three out of the eight characteristic species were among the five most dominant species of this site, while the other five species simply contributed to habitat specificity. The dominant species of most other sites were eurytopic species. These results imply that cultivation and, to a lesser degree, affor-

estation altered the species composition of the community, while this is not the case with grazing.

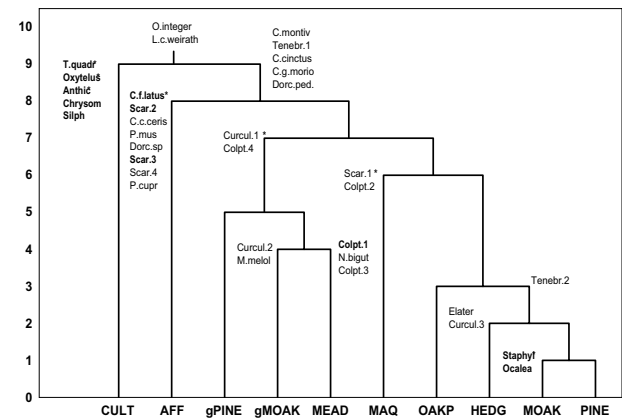


Fig. 3. – Dendrogram presenting the indicator species of each sampling site, identified by IndVal. Significant indicator species are noted by * (p<0.05). Names in bold indicate species that dominate the corresponding site. For site codes see Table 1. Species names are listed in Table 2.

TABLE 2

Species indicator values for the corresponding clustering level, i.e. the site or group of sites where the species exhibits maximum indicator value. Statistical significance is also indicated (p<0.05)

Species list	IndVal	sites	
Carabidae			
<i>Trechus (Trechus) quadristriatus</i> (Schränk, 1781)	58.45	CULT	*
<i>Calathus (Calathus) fuscipes latus</i> Audinet-Serville, 1821	44.47	AFF	*
<i>Carabus (Procrustes) coriaceus cerisyi</i> Dejean, 1826	31.13	AFF	ns
<i>Laemostenus (Pristonychus) cimmerius weiratheri</i> G. Müller, 1931	22.03	all sites	ns
<i>Notiophilus (Latviaphilus) biguttatus</i> (Fabricius, 1779)	18.62	MEAD	ns
<i>Calathus (Neocalathus) cinctus</i> (Motschulsky, 1850)	18.52	all uncultivated sites	ns
<i>Carabus (Pachystus) graecus morio</i> Mannerheim, 1830	16.67	all uncultivated sites	ns
<i>Carabus (Archicarabus) montivagus</i> Palliardi, 1825	37.04	all uncultivated sites	ns
Staphylinidae			
<i>Oxytelus</i> sp.	47.85	CULT	*
Staphylinidae unid.	29.22	MOAK	*
<i>Ocyopus integer</i> Abeille, 1900	28.81	all sites	ns
<i>Pseudocypus (s. str.) mus</i> Brulle, 1832	26.49	AFF	ns
<i>Ocalea</i> sp.	23.22	MOAK	ns

TABLE 2 (cont.)

Species indicator values for the corresponding clustering level, i.e. the site or group of sites where the species exhibits maximum indicator value. Statistical significance is also indicated ($p < 0.05$)

Species list	IndVal	sites	
<i>Pseudocypus (s. str.) cupreus</i> Rossi, 1790	13.01	AFF	ns
Scarabaeidae			
species unid.1	33.57	MAQ	*
species unid.2	32.54	AFF	ns
species unid.3	15.96	AFF	ns
species unid.4	14.86	AFF	ns
<i>Melolontha melolontha</i> (Linnaeus, 1758)	12.29	gMOAK	ns
Curculionidae			
species unid.1	33.33	gPINE, gMOAK, MEAD	*
species unid.2	21.76	gMOAK	ns
species unid.3	11.49	HEDG	ns
Cerambycidae			
<i>Dorcadion</i> sp.	23.24	AFF	ns
<i>Dorcadion cf. pedestre</i> (Poda, 1761)	12.96	all uncultivated sites	ns
Anthicidae			
species unid.	39.1	CULT	*
Silphidae			
species unid.	10.56	CULT	ns
Elateridae			
species unid.	16.85	HEDG	ns
Chrysomelidae			
species unid.	19.4	CULT	ns
Tenebrionidae			
species unid.1	25.93	all uncultivated sites	ns
species unid.2	16.67	forested sites and HEDG	ns
Families unidentified			
species unid.1	20.86	MEAD	ns
species unid.2	9.09	MAQ	ns
species unid.3	15.9	MEAD	ns
species unid.4	13.56	gPINE, gMOAK, MEAD	ns

DISCUSSION

Grazing

Our results showed that the diversity of the coleopteran community was much higher in the grazed than in the undisturbed part of both the deciduous and the pine forest, a result also reported by INGS & HARTLEY (1999) for carabid assemblages of forest environments. This increase of diversity may be attributed to several factors that affect the coleopteran communities, such as the light (FAHY & GORMALLY, 1998) that penetrates the overstorey, the development of ground vegetation (INGS & HARTLEY, 1999), and most importantly the high degree of structural heterogeneity induced by grazing (GARDNER et al., 1997) and the consequent changes of microclimatic conditions (RODRIGUEZ et al., 1998). Moreover, the grazed pine forest is actually a forest edge, while the overgrazed meadow is the other extreme of the forest-grass spectrum. Increased diversity of the coleopteran fauna in forest edges has been well established (MAGURA et al., 2000b; HORVATH et al., 2002). In the overgrazed grass covered meadow, diversity was higher than that recorded at the undisturbed site but lower than that recorded at the moderately grazed site. Indeed, too much grazing reduces structural variation of vegetation and thus diversity of coleoptera (GARDNER et al., 1997), and as CONNELL (1978) pointed out, medium disturbance may indeed enhance diversity.

Diversity increase due to grazing was accompanied by changes in the hierarchical structure of the community. In the natural forest, one species over-dominated the community and almost all the others were represented by very low numbers, while in the grazed site dominance was shared by several species. As far as we know, up to now, only MOLINA et al. (1999) have reported the dominance of a single species within the forest catches as a reason accounting for the low diversity of the forest ground-dwelling community. In line with their work, we believe that the mosaic structure of vegetation at the grazed sites offers a variety of microhabitats where soil arthropods may establish and increase their local population size. Indeed, in the mediterranean pastureland, which is the most heterogeneous of all our sampling sites due to the variety of shrub species, we recorded the most diverse and hierarchically-structured community.

Regarding the species composition of the coleopteran community, according to our results, it does not seem to alter due to grazing. ELEK et al. (2001) state that the movement of forest species is prevented in more grassy sites, while RODRIGUEZ et al. (1998) claim that the habitat breadth of species correlates with the degree of disturbance at a site. However, the IndVal analysis did not reveal any characteristic forest species that disappeared in the grazed sites or vice versa, since the dominant species of both natural and grazed forests were eurytopic.

Cultivation

Apart from grazing, cultivation also had a positive result on the diversity of the coleopteran community. However, the only component of diversity that increased from the natural forest to the adjacent cultivated field was the number of species, while no pronounced changes in

the community structure were recorded, as was the case with grazing. BOHAC (1999) and KROMP (1999) have also reported high species numbers of Coleopterans in arable habitats. We should also note that in the wheat cultivation that we studied there was no insecticide application, which is known to have detrimental effects for several families of beetles (WILSON et al., 1999). Moreover, the existence of the natural hedgerow at the edge of the field is very important for maintaining biodiversity, since it acts as a refuge for overwintering field species (KROMP, 1999), or relict woodland species (ASTERAKI et al., 1995), from where beetles may reinvade the adjacent field in response to changing field conditions (VARCHOLA & DUNN, 1999).

The most important effect of cultivation recorded in this study was the changes in species composition. Such changes are also reported by KROOSS & SCHAEFER (1998). SIEREN & FISCHER (2002) state that arable land is a suitable habitat for eurytopic species without special ecological preferences. However, the field of our study was dominated by stenotopic indicator species, the number of which was the highest one recorded at all sampling sites. This is again a completely different effect from the one induced by the previous human intervention, i.e. grazing.

Afforestation

As regards the effect of afforestation on the community patterns of Coleoptera, this was intermediate compared with the effects of grazing and cultivation. The afforested site was more diverse than the natural pine forest, regarding both the species number and the equitability. Thus, high diversity was accompanied by changes in community structure, although the latter were not as striking as the ones recorded at grazed sites. Furthermore, apart from the cultivated field, which had a completely different species composition from all other sampling sites, the coleopteran community of the afforested site was clearly discernible as well.

Our results are quite different from those of ELEK et al. (2001), who found a more abundant and species rich carabid assemblage in a native forest than in a conifer plantation. However, the fact that the native forest that they studied was a deciduous one, might be a possible explanation. Besides, there is both a geographical and a habitat associated variation in the effects of afforestation on coleopteran communities (BUTTERFIELD et al., 1995). For example, FAHY & GORMALLY (1998) imply that the low carabid diversity that they found in a conifer plantation is related to low plant species richness and consequently to low food availability, but they state that the inclusion of open areas within plantations will increase available microhabitats and thus coleopteran diversity. Indeed, in the pine plantation of our study there is no dense overstorey, because the trees are about 7 years old and of low height, and thus there are still grass covered areas between them. Based on findings of INGS & HARTLEY (1999), who believe that in mature forests or even plantations, it is the shady and humid microclimate that species are responding to, we speculate that the alteration of shade and soil moisture due to the eventual growth of trees will lead to an homogeneous microclimate and to an adverse effect on coleopteran diversity. Such an effect is

reported also by KOIVULA et al. (2002) and MAGURA et al. (2002).

CONCLUSIONS

To sum up, although the three management practices increased the diversity of epiedaphic Coleoptera, their effects on the community organization patterns differed. Grazing did not affect the species composition of communities but altered the community structure. The communities of the ungrazed forests were over-dominated by one species, while those of the grazed sites were hierarchically structured. On the other hand, the main effect of cultivation on the coleopteran communities was the profound change in species composition. The cultivated site was dominated by characteristic species that were almost absent from all other sites. Afforestation caused intermediate changes in both community structure and composition.

The use of a community measure to track habitat changes is an important alternative to assessments focused on single species (MATTONI et al., 2000). Our results show that although certain species of Coleoptera had significant indicator value and seemed to be good indices for assessing human impacts on natural environments, the study of changes in the community organization patterns is even more appropriate.

ACKNOWLEDGEMENTS

We are indebted to Dr. Borislav Gueorguiev and Mr. Ognyan Mikov from the National Museum of Natural History (Sofia, Bulgaria) for identifying our Coleoptera specimens. We also wish to thank WWF-Hellas for financing this work.

REFERENCES

- ASTERAKI, E.J., C.B. HANKS & R.O. CLEMENTS (1995). The influence of different types of grassland field margin on carabid beetle (Coleoptera, Carabidae) communities. *Agr. Ecosyst. Environ.*, 54 : 195-202.
- BAUR, B., S. ZSCHOKKE, A. CORAY, M. SCHLAPFER & A. ERHARDT (2002). Habitat characteristics of the endangered flightless beetle *Dorcadion fuliginator* (Coleoptera : Cerambycidae) : implications for conservation. *Biol. Conserv.*, 105 : 133-142.
- BOHAC, J. (1999). Staphylinid beetles as bioindicators. *Agr. Ecosyst. Environ.*, 74 : 357-372.
- BUTTERFIELD, J., M.L. LUFF, M. BAINES & M.D. EYRE (1995). Carabid beetle communities as indicators of conservation potential in upland forests. *Forest Ecol. Manag.*, 79 : 63-77.
- CONNELL, J.H. (1978). Diversity in tropical rainforests and coral reefs. *Science*, 199 : 1302-1310.
- DUFRENE, M. & P. LEGENDRE (1997). Species assemblages and indicator species : the need for a flexible asymmetrical approach. *Ecol. Monogr.*, 67 : 345-366.
- ELEK, Z., T. MAGURA & B. TOTHMERESZ (2001). Impacts of non-native Norway spruce plantation on abundance and species richness of ground beetles (Coleoptera : Carabidae). *Web Ecol.*, 2 : 32-37.
- FAHY, O. & M. GORMALLY (1998). A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. *Forest Ecol. Manag.*, 110 : 263-273.

- GARDNER, S.M., S.E. HARTLEY, A. DAVIES & S.C.F. PALMER (1997). Carabid communities on heather moorlands in north-east Scotland: The consequences of grazing pressure for community diversity. *Biol. Conserv.*, 81 : 275-286.
- HORVATH, R., T. MAGURA, G. PETER & B. TOTHMERESZ (2002). Edge effect on weevils and spiders. *Web. Ecol.*, 3 : 43-47.
- HUMPHREY, J.W., C. HAWES, A.J. PEACE, R. FERRIS-KAAN & M.R. JUKES (1999). Relationships between insect diversity and habitat characteristics in plantation forests. *Forest Ecol. Manag.*, 113 : 11-21.
- INGS, T.C. & S.E. HARTLEY (1999). The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *Forest Ecol. Manag.*, 119 : 123-136.
- KOIVULA, M., J. KUKKONEN & J. NIEMELA (2002). Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation*, 11 : 1269-1288.
- KROMP, B. (1999). Carabid beetles in sustainable agriculture : a review on pest control efficacy, cultivation impacts and enhancement. *Agr. Ecosyst. Environ.*, 74 : 187-228.
- KROOSS, S. & M. SCHAEFER (1998). The effect of different farming systems on epigeic arthropods : a five-year study on the rove beetle fauna (Coleoptera : Staphylinidae) of winter wheat. *Agr. Ecosyst. Environ.*, 69 : 121-133.
- MAGURA, T., V. KODOBOCZ & ZS BOKOR (2001). Effects of forestry practices on carabids (Coleoptera : Carabidae)-implications for nature management. *Acta Phytopathologica et Entomologica Hungarica*, 36(1-2) : 179-188.
- MAGURA, T., B. TOTHMERESZ & ZS. BORDAN (2000a). Effects of nature management practice on carabid assemblages (Coleoptera : Carabidae) in a non-native plantation. *Biol. Conserv.*, 93 : 95-102.
- MAGURA, T., B. TOTHMERESZ & T. MOLNAR (2000b). Edge effect on carabid assemblages along forest-grass transects. *Web Ecol.*, 2 : 7-13.
- MAGURA, T., B. TOTHMERESZ & Z. ELEK (2002). Impacts of non-native spruce reforestation on ground beetles. *Eur. J. Soil Biol.*, 38 : 291-295.
- MATTONI, R., T. LONGCORE & V. NOVOTNY (2000) Arthropod Monitoring for Fine-Scale Habitat Analysis : A Case Study of the El Segundo Sand Dunes. *Environ. Manag.*, 25(4) : 445-452.
- MAY, R.M. (1975). Patterns of species abundance and diversity. In : CODY M.L. & J.M. DIAMOND (eds), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA : 81-120.
- MOLINA, S.I., G.R. VALLADARES, S. GARDNER & M.R. CABIDO (1999). The effects of logging and grazing on the insect community associated with a semi-arid chaco forest in central Argentina. *J. Arid Environ.*, 42 : 29-42.
- MOTOMURA, I. (1932). A statistical treatment of associations (in Japanese and cited in MAY 1975). *Jpn. J. Zool.*, 44 : 379-383.
- PETIT, S. & M.B. USHER (1998). Biodiversity in agricultural landscapes : The ground beetle communities of woody uncultivated habitats. *Biodivers. Conserv.*, 7(12) : 1549-1561
- RENYI, A. (1961). On measures of entropy and information. In : NEYMAN, J. (ed.), *Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability*, Vol 1. University of California Press : 547-561.
- RICOTTA, C. (2000). From theoretical ecology to statistical physics and back : self-similar landscape metrics as a synthesis of ecological diversity and geometrical complexity. *Ecol. Model.*, 125 : 245-253.
- RODRIGUEZ, J.P., D.L. PEARSON & R. BARRERA (1998). A Test for the adequacy of bioindicator taxa : are tiger beetles (Coleoptera : Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela ? *Biol. Conserv.*, 83(1) : 69-76.
- SIEREN, E. & F.P. FISCHER (2002). Evaluation of measures for enlargement, renaturation and development of a dry grassland biotope by analysing differences in the carabid fauna (Coleoptera). *Acta Oecologica*, 23 : 1-12.
- TOTHMERESZ, B. (1995). Comparison of different methods for diversity ordering. *J. Veg. Sci.*, 6 : 283-290.
- VARCHOLA, J.M. & J.P. DUNN (1999). Changes in ground beetle (Coleoptera : Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation. *Agr. Ecosyst. Environ.*, 73 : 41-49.
- WILSON, J.D., A.J. MORRIS, B.E. ARROYO, S.C. CLARK & R.B. BRADBURY (1999). A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agr. Ecosyst. Environ.*, 75 : 13-30.