THE IMPACT OF HUMAN LAND USE ON THE COMPOSITION AND RICHNESS OF GROUND AND DUNG BEETLE ASSEMBLAGES

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Abstract. This paper presents the results of a survey on the habitat and seasonal variation in activity density and richness of ground and dung beetle assemblages in a heterogeneous landscape of central Greece. Beetles were collected using 2,646 pitfall traps across an area of 138 ha representative of the Mediterranean mountainous landscape. Sampling was performed in cereal fields, corn fields, fallow land, grassland, *Robinia pseudoacacia* plantations, oak forest - farmland ecotone and oak forest using pitfall traps. A total of 18,275 individuals belonging to 38 species were collected, whereas only seven species constituted the 82.64% of the overall captures. *Onthophagus ovatus* was the most common species in all habitats. Beetle assemblages varied markedly regarding the number of species, while higher densities were reported during June. Significant differences in beetle richness were found considering habitat preferences with the lowest species richness in corn fields. Carabidae assemblages were both most abundant and diverse in plantations, whereas Scarabaeidae assemblages were most abundant and diverse in fallow land. Among estimated diversity indices, Margalef's index generated similar results with the observed diversity, likewise non parametric estimators. Overall, the results obtained in the present study suggest that agricultural areas in mountainous heterogeneous landscape might be the important factor for conserving rich beetle diversity, whereas supplementary biotic factors should be explored.
Keywords: *Mediterranean ecosystems; Carabidae; Scarabaeidae; habitat heterogeneity; correspondence analysis*

Introduction

Epigeic invertebrates have been successfully used as biological indicators of ecosystem health and habitat evaluation in a variety of studies (Redolfi et al., 1999; Vanbergen et al., 2005; Liu et al., 2006) focusing either on specific species or families or even on the whole order. A considerable effort has been invested in various aspects of their ecology, especially regarding effects of habitat heterogeneity and habitat loss on their activity density and distribution (Driscoll and Weir, 2005), and effects of the geographical location on their population sustainability (Thomas et al., 2001; Holland et al., 2004).

Among epigeic invertebrates, the most common ones are ground (Carabidae) and dung (Scarabaeidae) beetles. Most commonly ground beetles constitute an important group for comparative ecological studies since they are abundant, their ecology and

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systematics are well known (Lövei and Sunderland, 1996) and are sensitive to habitat changes as well (Niemelä et al., 1993). In addition, they are easily collected, allowing a standardized successful sampling, while some are highly selective and restricted to a particular habitat (Niemelä et al., 1992). Dung beetles though have proved to be key organisms in nutrient poor systems (Piñero and Avila, 2004), aerating and softening the soil (Brusaard, 1987; Herrick and Lal, 1996). However, only recently have they received increasing attention as indicators of changes in land use (Spector, 2006; Barragan et al., 2011) and the health status of pastures (Davis et al., 2004). Nonetheless, they have been scarcely studied in the Mediterranean region, except for some western European regions (France and Iberian Peninsula) and the western Rhodopes Mountains of Greece (Lobo et al., 2007). Wassmer (1995) studied the habitat selection of coprophagous beetles in southwestern Germany resulting in main differences comparing to other investigations from other geographic latitudes reflecting the variability within widely distributed species which are an ultimate reason for their expansion.

Several recent studies are dealing with beetle diversity in mountain landscapes of different geographical areas such as Iberian Peninsula (Lobo and Martin-Piera, 1999; Zamora et al., 2007) and a forested landscape of Mexico (Navarette and Halffter, 2008). It seems that habitat type and structure drive local species richness (Tews et al., 2004), whereas habitat heterogeneity is positively correlated with high diversity levels (Brose, 2003). Moreover, several studies have recorded higher diversity levels in agriculture unit (da Silva, 2008), tallgrass prairies (Larsen et al., 2003), mown meadows and riparian woodlands (Gutiérrez et al., 2004) than in other habitats. Contrasting results could reflect differences in habitat heterogeneity between study areas so there is a need for a closer examination of the effect of habitat heterogeneity on beetle diversity. Furthermore, forest edges with increased beetle species richness substantiate a significant edge effect (Báldi and Kisbenedek, 1994; Magura, 2002).

Despite the fact that Mediterranean area is one of the world's richest regions in terms of animal and plant diversity (Myers et al., 2000; Verdú et al., 2000; Atauri and de Lucio, 2001; Burel et al., 2004; Cuttelod et al., 2008), there is only a handful of studies dealing with beetle distribution in upland landscapes of Greece. For example, Trichas (1997) studied the ecology and biogeography of ground coleoptera in the southern Aegean area, with emphasis on seasonal composition of Carabidae and Tenebrionidae assemblages, Anastasiou and Legakis (2002) studied the distribution of Carabidae in some mountains of Peloponnese, southern Greece, whereas Pitta (2009) studied the communities of soil arthropods in a mosaic of sites in different succesional stages on mountain Parnitha after fire. In northern Greece, Argyropoulou et al. (2005) described and compared the community organization patterns of Coleoptera in various sites of the Dadia forest reserve, regarding different types of vegetation and management practices. Although these studies have led to a better understanding of beetle diversity, even fewer studies have focused on seasonality and assemblage structure of ground and dung beetles (Theile, 1977; Jay-Robert et al., 1997; Errouissi et al., 2004). Finally, there has been no investigation on the relative contribution of cereal cultivation and adjacency with semi-natural habitats in mountainous landscapes on beetle richness. This lack of knowledge could lead to unsustainable land use management, as these insects play a crucial role in many ecosystem functions.

The aim of the current paper was to study the relationship between habitat heterogeneity and beetle richness in an upland Mediterranean landscape where agriculture is dominated by cereals. The specific objectives of the study were to

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investigate: (1) the species diversity of the landscape using beetles as an indicator taxon, (2) the seasonal distribution patterns of ground and dung beetle assemblages throughout their activity season; (3) whether habitat haterogeneity influences beetle species richness across cereal fields and neighbouring semi-natural habitats and (4) whether ground and dung beetle assemblages respond similarly to habitat heterogeneity.

Materials and methods

Study area

The study was conducted in a heterogeneous Mediterranean landscape of western Thessaly, in central Greece (Flabouresi, 33 km NE of Kalabaka town), (39°50΄44΄΄N and 21°42΄30΄΄W) (*Fig. 1A*). The study area is part of the Natura 2000 site "Antichasia - Meteora Mountains", which is considered as an important area for bird species of european conservation concern (Meliadis and Kassioumis, 2001), the endemic plant species *Centaurea kalambakensis* (Freyn & Sint) and *Centaurea lactiflora* (Halácsy) (Asteraceae) and endangered insects such as *Rhysodes sulcatus* (Dalman) (Carabidae) (Legakis and Maragou, 2009).

The area of Flabouresi (altitude ≈ 800 m above sea level) consists of a mosaic of agricultural fields (412 ha) (*Fig.1B*) surrounded by forests dominated by *Quercus pubescens* (Willdenow) (Fagaceae). The topography of the southern slopes is moderate (average slope < 30°), whereas all other slopes are relatively low (average slope < 15°). The climate is characterized as typical sub-Mediterranean, with warm, dry summers, and mild, wet winters. The average monthly temperature ranges from 15.5 °C (January) to 26.9 °C (August), while the annual rainfall averages ≈ 700 mm (data from Kalabaka Meteorological Station, 27 km away). The dry period lasts from middle June to middle September.

Livestock (sheep, goats and cattle) grazing, along with agriculture, are the main productive activities of the area. The fieldwork was conducted in a total area of 138 ha:

- 61 ha of dry winter wheat [(Triticum aestivum Linnaeus (Poaceae)]), planted in mid September and harvested in late July;
- 6 ha of dry corn fields [(Zea mays Linnaeus (Poaceae)], planted in late May and harvested in late August;
- 9 ha of fallow land, plowed agricultural land unseeded for two or more growing seasons with short vegetation cover;
- 27 ha grazed grasslands, non fertilised, including mostly Anthemis arvensis, Avena fatua, Convolvulus arvensis, Lolium sp., Poa annua, Poa pratensis; Senecio vulgaris and Vicia cracca;
- 12 ha of managed Robinia pseudoacacia Linnaeus (Fabaceae) plantations, 10-year old trees up to 8-10 m high;
- 8 ha oak forest, 15-year old trees up to 15-20 m high dominated by Quercus pubescens, Q. frainetto and Q. ithaburensis var. cerris forming a sparse forest and
- 15 ha oak forest - farmland ecotones adjoining forests with other habitats.

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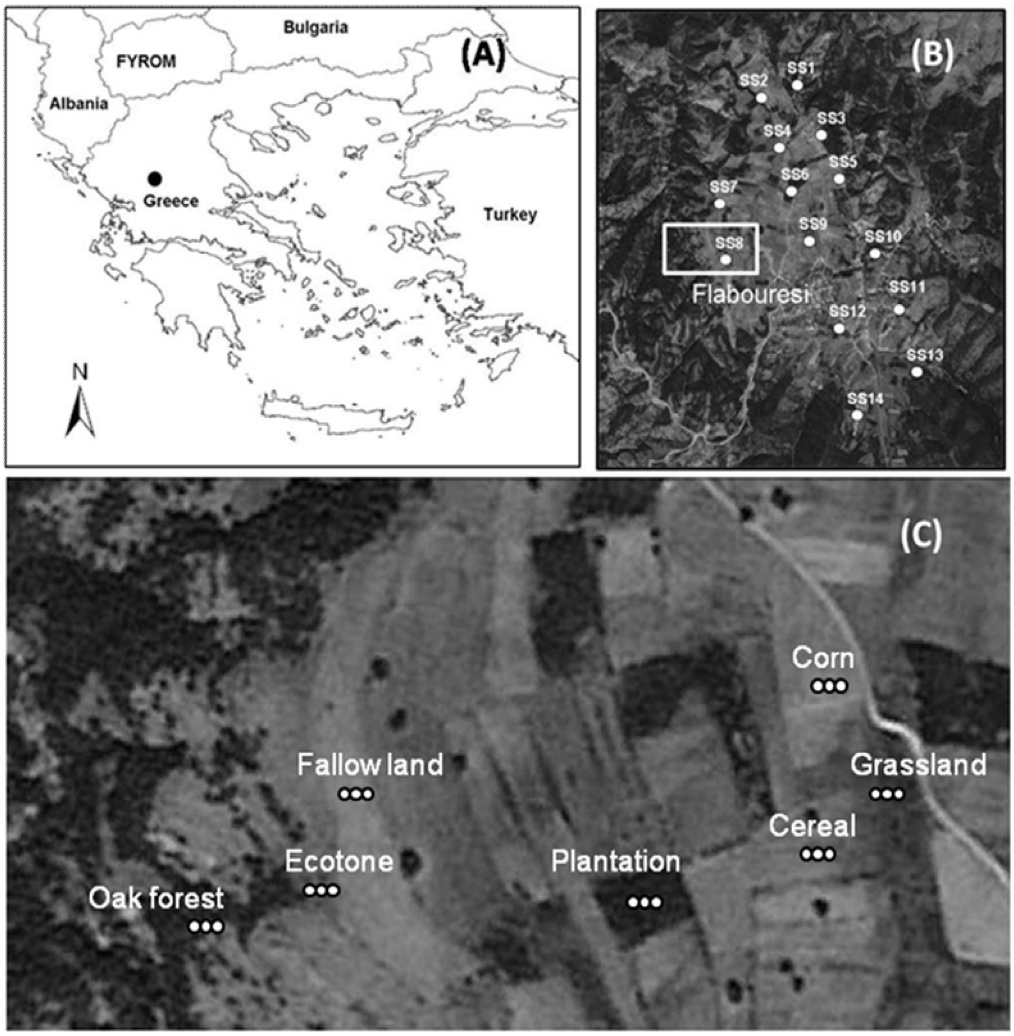

***Figure 1**. a) The study area, b) the 14 sampling sites (SS) and c) the sampling design of the pitfall traps at one of the 14 sampling sites*

Beetle sampling

Beetles were sampled at 14 sites (*Fig. 1B*) using plastic pitfall traps (diameter 9 cm, depth 13 cm) filled with 250 ml water plus 0.25% household vinegar (5% acetic acid) as a preserving solution (Thomas and Marshall, 1999). Each sampling site included all 7 habitats (see above). Pitfall traps were used to sample beetles as a very convenient and easy-to-operate method, yielding highly standardised samples (Southwood and Henderson, 2000). Collected samples (3 traps x 7 habitats x 14 sites x 9 months = total 2,646 traps) (*Fig. 1C*) were analysed in the laboratory. The distance between each trap was ≈ 10 m, for avoiding inter trap effects (Digweed et al., 1995), and within 10 m of each habitat fragment, so that trap catches represent the assemblage within that habitat. Pitfall traps were placed from 25 May 2006 until 15January 2007 for two consequent days (48 h) per month, to prevent oversampling that might have an excessive impact on the density of beetles and minimize depletion of the insect fauna. All pitfall traps were placed so that the lip of the cup to be slightly below of the ground surface in a fixed position throughout the sampling period. In few cases during the trapping period the

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solution was diluted by rainwater, but none of the traps overflowed. Five traps from the grasslands and 7 from the fallow land were excluded due to the severe damage by grazing animals. The geographical position of each pitfall trap was recorded using a global positioning system (GPS; e-Trex Vista, Garmin Co. Ltd.). Adult specimens were taken to the laboratory and identification to species level was accomplished using dichotomus keys (Chinery, 1993; Gueorguiev and Gueorguiev, 1995; Chinery, 2000) following the nomenclature of Fauna Europaea (Vigna-Talianti, 2007).

Statistical analysis

The numerical importance of each species in the structure of the whole community was computed by the total number of captured individuals (N), the relative activity density (%) and the species occurrence (%O) defined as the pure records of locations where a species occurred (Tsoar et al., 2007). To compare the variation of beetle assemblages among the different habitat types, the total number of activity densities and number of species per three trap complex (within habitat within site) were used. Values of variables were compared by an ANOVA, followed by the Tukey's *b* test. If assumptions of normality and homogeneity of variances (using Kolmogorov–Smirnov test and *F* test respectively, Sokal and Rohlf, 1995), were not met, data were transformed according to the method Box-Cox (Draper and Cox, 1969).

Although species richness is generally the most relevant component of the beetle diversity, alpha diversity was also calculated by three indices: i) the Shannon-Weiner index (H') (Shannon and Weaver, 1949), despite its sensitivity to the presence of rare species: $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of the ith species among the total collected; ii) the Berger-Parker's index (BPI), which is a measure of the numerical importance of the most abundant species: $BPI = N_{max} / N$ where N_{max} is the number of individuals of the most abundant species, and N is the total number of individuals in the sample; and iii) Margalef's diversity index (D_{Mg}), which balances the richness by the beetle numbers (Magurran, 1988): $D_{Mg} = (S-1) / \ln N$, where S is the number of species and N is the number of individuals.

To estimate species richness instead of the observed number of species (Brose, 2002; Chao, 2005), we tested the following four nonparametric estimators: i) Chao 2, ii) 1st Order Jacknife, iii) 2nd Order Jacknife and iv) Bootstrap. These nonparametric species richness estimators use the sample-based data to estimate the total number of species (Gotelli and Colwell, 2001; Chao and Bunge, 2002). All alpha diversity and nonparametric indices were generated using the software Species Diversity and Richness ver. 4.0 (PISCES Conservation Ltd 2006). The randomization test of Solow (1993) and the t-test were used to assess the significance of differences in diversity and richness along the different habitat types at the significance level 0.05.

To investigate the seasonal patterns of both beetle families mean values (± SE) of activity densities and species richness were calculated and presented graphically per month. To analyse the variation over time in activity densities and species richness of ground and dung assemblages along the various habitat types, repeated measures ANOVA was used followed by the Tukey's *b* test. The model included "habitat type" being the fixed factor (seven levels: cereal, corn, fallow, grassland, *Robinia pseudoacacia* plantation, oak forest - farmland ecotone and oak forest), "season" being the repeated factor (seven out of nine sampling periods, since there was no pitfall catches in December and January) and the interaction between the two variables. All

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data analyses were performed using the PASW Statistics 19 (SPSS Inc., Chicago, USA).

To explore the beetle compositional variation and find possible differences among different habitats, Correspondence Analysis (CA) (ter Braak and Smilauer, 2002) and the xlstat v. 2011.3.02 statistical analysis software (http://www.xlstat.com) were used. The multivariate data of species composition of the census points were analyzed by CA, which ordinated individual samples in a way that the differences among them would be maximized. Correspondence analysis was applied to the species x trap catches in order to reveal the relationships between a species and trap locations.

Results

Species composition and richness

A total of 18,275 adult beetles belonging to 38 species and 20 genera were collected throughout the sampling period (*Table 1*). A percentage of approximately 0.24 % of the whole captured specimens was not identified to species level because they had decayed in the trap. The number of singletons (species with only one individual) was 5 carabids, while the captured doubletons (species with only two individuals) were 2 carabids and 1 scarabid in the total 2,646 traps. The most abundant subfamilies in terms of the number of individuals recorded were: Scarabaeinae (N=15,706), Harpalinae (N=1,958) and Carabinae (N=559). The most numerous in terms of number of species within ground and dung beetle assemblages in comparison to all other genera were the genus *Pterostichus* and *Onthophagus*, respectively. Regarding ground beetle assemblages, the most frequently occurring species were: *Pterostichus nigrita* (Paykull), *P. cupreus* (Bonelli), *Carabus nemoralis* (Linnaeus) and *Myas chalybaeus* (Palliardi), whereas *Onthophagus ovatus* (Linnaeus), *O. coenobita* (Herbst) and *Gymnopleurus mopsus* (Pallas) were the most abundant dung beetles. *Zabrus tenebrioides* (Goeze), which is the most important pest for cereals of the captured species, was firstly captured in late July in the *R. pseudoacacia* plantations. A total of 67 individuals were captured throughout the entire sampling period. During the same period only 2 to 3 individuals of the species were captured in wheat and corn respectively. Twenty four out of the 38 species were classified as rare species representing less than 0.1% of all beetles collected (*Table 1*). Some of the most abundant species were captured in a small proportion of traps. For example, 2,086 individuals of *O. coenobita* were captured in 69 pitfall traps.

Habitat effects

Significantly different beetle richness was detected among habitats denoting habitat preferences (carabid species richness, $F = 7.548$, $p < 0.0001$; scarabid species richness, $F = 10.397$, $p < 0.0001$), whereas both assemblages exhibited the lowest species richness in corn fields (*Table 2*). Regarding the ground beetle assemblage, the highest number of species was recorded in grasslands, whereas similar number of dung beetle species was counted in fallow land. Oak forest was completely dominated by three species: *C. nemoralis* (total number of captured individuals N=141), *O. ovatus* (N=162) and *M. chalybaeus* (N=141). *O. ovatus* was also common in all other habitats, whereas the other two species occurred mostly in the oak forest. Similarly, significantly different beetle activity densities were found among habitats showing their habitat preferences

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(carabid activity density, $F = 5.986$, $p < 0.0001$; scarabid activity density, $F = 6.543$, $p < 0.0001$). Most common scarabids were captured within the plantations, whereas dung beetles were dominant in the catches from the fallow land.

***Table 1**. Overview of individuals trapped in the different habitats in pitfall traps in Flabouresi during 2006 (n=294). N: Total number of captured individuals; %: Relative activity density of each species in relation to the total number; f: Number of pitfall traps where the species was trapped, and O: species occurrence (in percentage) in total sampled traps*

Family	Species	Habitat							Total	%	f	%O
		Cereal fields	Corn fields	Fallow land	Grassland	Plantations	Ecotone	Oak forest				
Carabidae	*Acinopus sp.* L.	-	-	-	-	-	2	-	2	0,01	2	0,68
	Amara similata G.	-	1	-	-	1	-	-	2	0,01	1	0,34
	Amara aenea De Geer	-	-	-	-	1	-	-	1	0,01	8	2,72
	Amara sp. B.	-	-	-	1	-	-	-	1	0,01	2	0,68
	Amara aulica P.	14	-	1	-	-	6	1	22	0,12	1	0,34
	Anchomenus dorsalis L.	1	1	-	1	1	-	-	4	0,02	4	1,36
	Brachinus crepitans L.	3	-	1	3	26	-	-	33	0,18	15	5,1
	Carabus coriaceus L.	25	17	19	27	47	43	7	185	1,01	102	34,69
	Carabus violaceus L.	7	5	37	8	22	26	7	112	0,61	48	16,33
	Carabus nemoralis M.	2	3	7	1	39	64	141	257	1,41	89	30,27
	Carabus sp. L.	5	-	-	-	-	-	-	5	0,03	1	0,34
	Cicindela campestris L.	-	-	1	9	-	1	-	11	0,06	7	2,38
	Harpalus zabroides D.	1	-	-	-	-	-	-	1	0,01	1	0,34
	Molops piceus P.	24	7	1	20	16	1	1	70	0,38	29	9,86
	Molops striolatus F.	7	1	-	5	-	-	-	13	0,07	3	1,02
	Myas chalybaeus P.	4	1	2	2	93	44	141	287	1,57	74	25,17
	Nebria sp. L.	-	-	-	-	1	1	1	3	0,02	5	1,7
	Poecilus sericeus F.	-	-	1	1	6	8	6	22	0,12	15	5,1
	Poecilus cursorius D.	2	-	-	10	-	-	-	12	0,07	7	2,38
	Poecilus purpurascens D.	-	-	-	3	1	-	-	4	0,02	2	0,68
	Poecilus punctulatus S.	7	-	8	1	22	8	12	58	0,32	32	10,88
	Poecilus sp. B.	-	-	-	-	-	-	1	1	0,01	7	2,38
	Pterostichus cupreus L.	120	46	34	169	107	13	23	512	2,8	113	38,43
	Pterostichus nigrita P.	155	37	100	168	237	34	14	745	4,08	136	46,26
	Rhysodes sulcatus F.	-	-	-	-	-	-	1	1	0,01	1	0,34
	Sphodrus sp.	1	39	2	2	29	16	32	121	0,66	33	11,22
	Zabrus tenebrioides Gze.	2	3	6	2	44	9	1	67	0,37	7	2,38
	Zabrus curtus A.S.	13	1	2	1	-	-	-	17	0,09		
Scarabaeidae	*Copris lunaris* L.	-	-	2	-	-	-	-	2	0,01	2	0,68
	Copris hispanus L.	-	-	6	-	1	-	-	7	0,04	4	1,36
	Gymnopleurus mopsus P.	231	-	350	125	32	72	1	811	4,44	62	21,08
	Onthophagus ovatus L.	2230	276	4451	3508	664	1115	162	12406	67,86	171	58,16
	Onthophagus coenobita Hbst.	267	3	366	614	50	724	62	2086	11,41	69	23,47
	Onthophagus amyntas O.	8	-	-	-	-	-	-	8	0,04	2	0,68
	Scarabaeus laticollis L.	-	-	1	-	-	1	1	3	0,02	3	1,02
	Scarabaeus sacer L.	8	-	37	8	2	11	-	66	0,36	28	9,52
	Scarabaeus semipunctatus F.	-	-	4	1	-	-	-	5	0,03	4	1,36
	Sisyphus scaefferi L.	33	-	69	42	34	84	50	312	1,71	19	6,46

Beetle diversity

The relationships between alpha diversity indices and the beetle assemblages among the habitat types varied significantly based on the randomization Solow test (*Table 2*). According to it, carabids were much more diverse in plantations similar to their activity densities. Low Shannon-Wiener index value was recorded in grasslands although most

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species were caught in this habitat. *BPI* values were high, meaning dominant species were recorded in this habitat resulting in great sensitivity of *H´* values, which was different from D_{Mg} since this is influenced by the rare species of the sample. Scarabids were significantly predominant and rich in fallow land and grasslands. On the contrary, corn fields were significantly poor with a total of only 2 species recorded. However, corn hosted one of the most dominant species (*O. ovatus*) (*Table 1*). Furthermore, Margalef's diversity index generated similar results with the observed ones, meaning the lowest value at the corn fields and the highest one at the fallow land.

***Table 2.** Comparison of activity densities, species richness, values of Shannon-Wiener index (H´), Berger-Parker Index (BPI), Margalef's diversity index (DMg) and estimated non parametric indices of species richness among the different habitats for the total sampling period. Significance of difference in indices values are indicated by the letters "a", "b", "c" and "d". Means followed by the same letter did not differ significantly (p = 0.05)*

Observation		Cereal fields	Corn fields	Fallow land	Grassland	Plantations	Ecotone	Oak forest
Carabidae	Abundance	380	164	215	426	692	263	383
	Species richness	19	14	17	21	18	15	15
	Individuals (mean ± SE)	0.97±0.21b	0.07±0.15b	0.55±0.08b	1.09±0.21a	1.76±0.23a	0.67±0.07b	0.97±0.17b
	Species (mean ± SE)	0.16±0.01b	0.12±0.02c	0.15±0.02b	0.16±0.01b	0.26±0.02a	0.22±0.01a	0.18±0.02b
	Alpha diversity indices							
	H´	1.93c	1.87c	2.41a	1.53d	2.13b	2.18b	1.61d
	BPI	0.35b	0.28b	0.20b	0.45a	0.32b	0.22c	0.37b
	D_{Mg}	3.03c	2.55d	3.91a	3.30b	2.60c	2.51c	2.35d
	Estimated non parametric indices of species richness (mean ± SE)							
	Chao 2	13.87±1.16a	12.56±2.20a	27.56±3.85b	14.45±1.34a	13.90±0.86b	13.15±0.55b	11.75±0.76b
	1st Order Jacknife	19.51±1.71b	15.14±1.38c	16.47±1.64a	21.08±2.15a	18.50±1.17b	15.02±0.82c	14.68±1.07c
	2nd Order Jacknife	22.46±2.43b	15.62±1.79c	19.55±2.37a	25.13±3.15b	19.58±1.95b	15.16±1.35c	16.48±1.67c
	Bootstrap	15.22±1.63a	11.24±1.34b	12.76±1.46a	16.16±1.98a	15.55±1.31b	13.56±1.14b	12.55±1.24b
Scarabaeidae	Abundance	2735	273	4746	4124	842	1854	279
	Species richness	6	2	9	6	6	6	5
	Individuals (mean ± SE)	19.53±0.44a	1.95±0.84c	33.9±9.29a	29.46±7.07ab	6.01±2.53c	13.24±4.44bc	1.97±3.33c
	Species (mean ± SE)	0.25±0.02a	0.08±0.01d	0.36±0.03a	0.33±0.04ab	0.20±0.03c	0.22±0.03bc	0.15±0.03cd
	Alpha diversity indices							
	H´	0.65a	0.06c	0.63c	0.59a	0.48c	0.80b	0.85b
	BPI	0.81d	0.98a	0.83a	0.81d	0.88a	0.58c	0.69c
	D_{Mg}	0.63a	0.17b	0.94b	0.60a	0.74b	0.66b	0.71b
	Estimated non parametric indices of species richness (mean ± SE)							
	Chao 2	4.82±0.28c	1.48±0.11d	7.48±0.39a	5.37±0.28b	4.64±0.28c	4.94±0.31c	3.97±0.25d
	1st Order Jacknife	6.51±0.39b	2.02±0.18d	9.06±0.61a	5.93±0.27b	5.97±0.42b	6.52±0.34b	5.02±0.42c
	2nd Order Jacknife	5.94±0.64b	2.37±0.38d	9.46±0.84a	5.66±0.44b	5.86±2.01b	6.37±0.62b	5.69±0.68c
	Bootstrap	4.96±0.45b	1.66±0.18d	7.42±0.68a	5.79±0.45a	5.18±0.49b	5.11±0.48b	4.18±0.42c

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Chao 2 and the Bootstrap generated estimates that were not higher than the observed richness, but 1st and 2nd Order Jacknife estimates, much more similar to each other, were much higher than the observed ones, irrelevant to the beetle family (*Table 2*). Regarding only Scarabaeidae assemblage, all non parametric indices generated the highest species richness at the fallow land and the lowest one at the corn fields. This is in total accordance with D_{Mg} index and the observed values. In addition, the nonparametric estimator Chao 2 showed the same performance as the index D_{Mg} referring to both Carabidae and Scarabaeidae assemblages.

Seasonal patterns of ground and dung beetle assemblages

The seasonal pattern of the 38 species and 18,275 individuals trapped through the sampling period is given in *Figure 2.* Both carabid and scarabid species richness was highest in June and September and lowest in November. Moreover, there was a high seasonal variation as far as scarabids was concerned between May (total number of individuals N = 270) and June (total number of individuals N = 11,149). In addition, during the mid July – September period, scarabids decreased and in turn carabids became predominant in the pitfall catches. Seasonal pattern of activity density was similar to that of species richness with its highest value in June and the lowest one in November. No pitfall catch occurred in December and January.

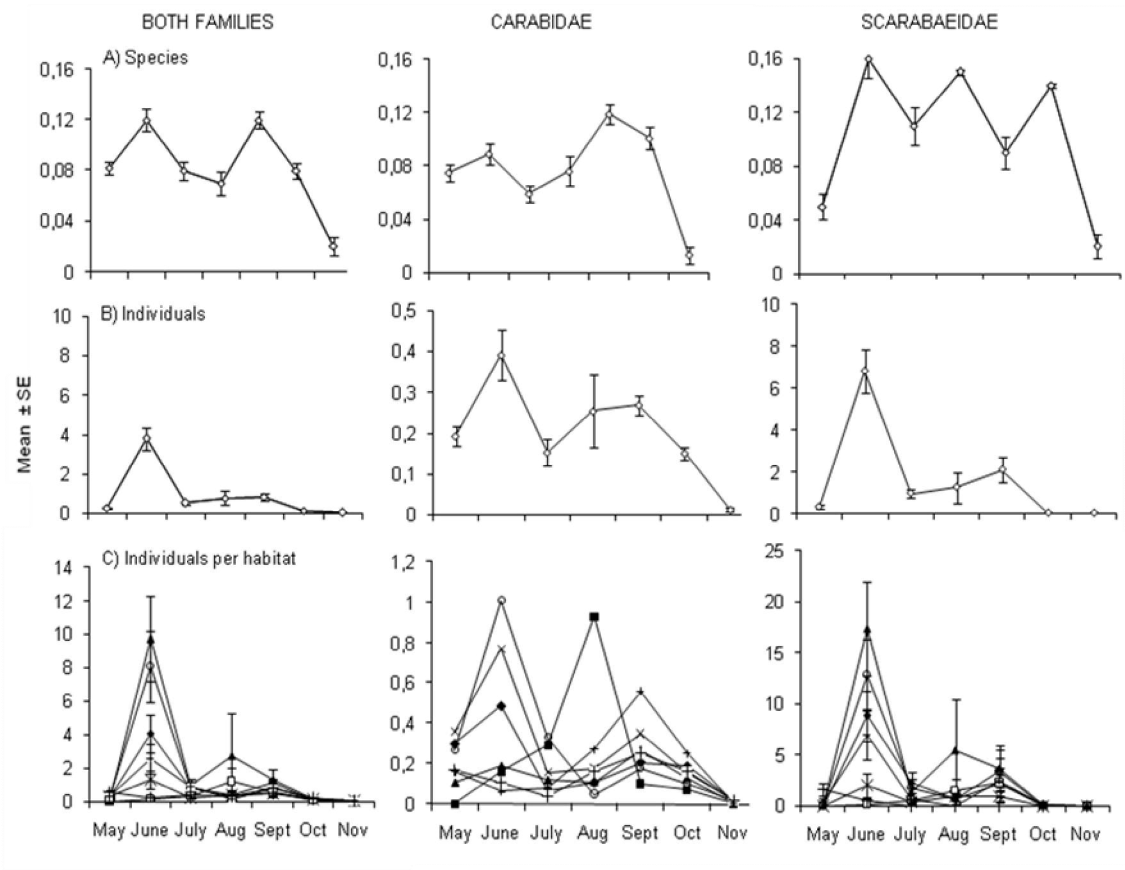

***Figure 2**. Seasonal patterns of the number of beetles: (A) mean species richness (±SE), (B) mean activity densities (±SE), and (C) mean activity densities per habitat type (±SE) (—◆—, cereal fields; —□—, corn fields; —▲—, fallow; —✕—, plantations; —○—, grassland; —+—, ecotone and —+— oak forest)*

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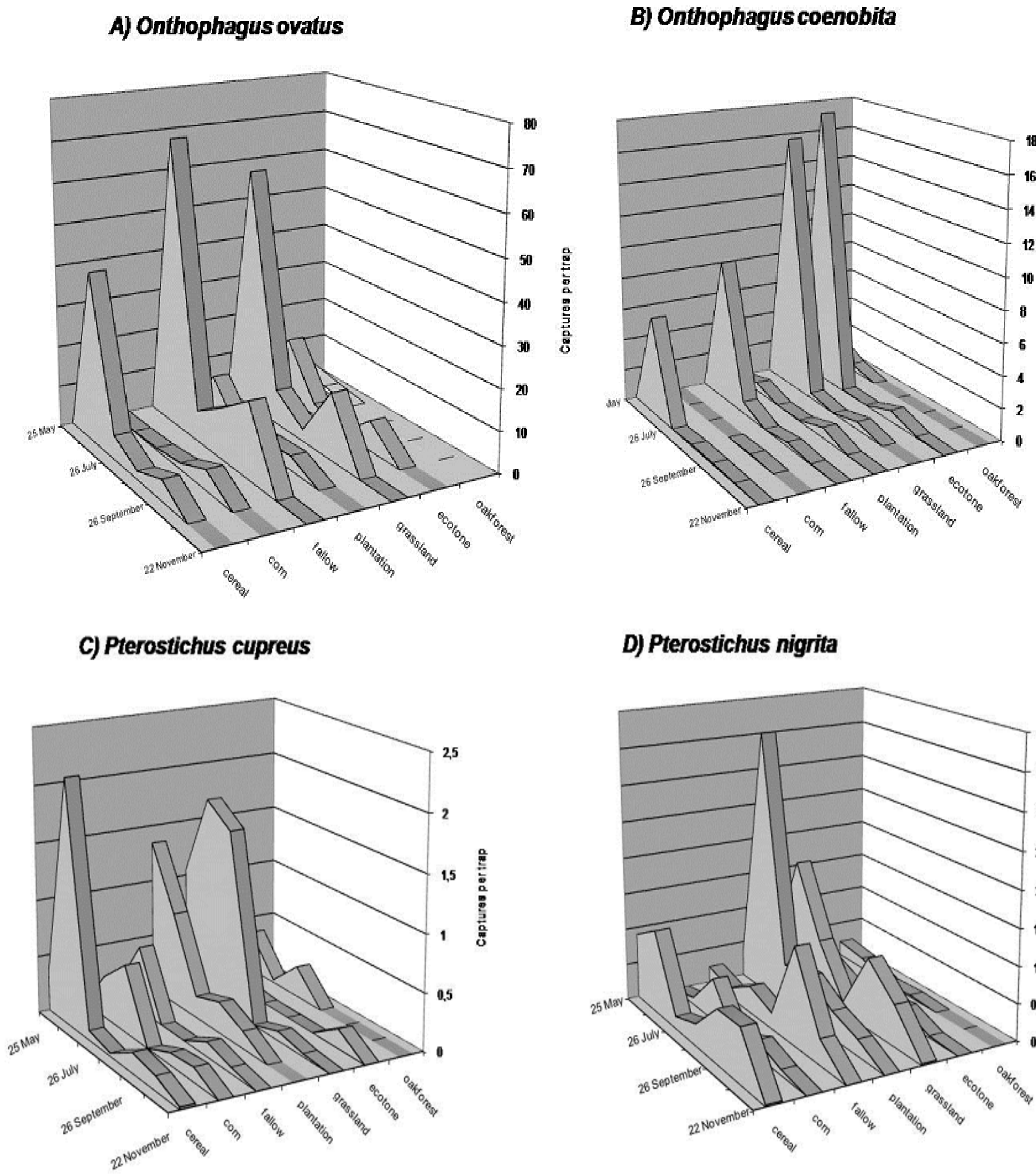
Based on seasonal activity recorded through the trapping period ground and dung beetles can be classified into two groups (*Fig. 3*).

Spring breeders appeared early in the season and their activity peaked from May until July. *O. coenobita* (*Fig. 3B*), *P. cupreus* (*Fig. 3C*) and *G. mopsus (Fig. 3F*) are characteristic species of that group. The second group, meaning *P. nigrita* (*Fig. 3D*) and *S. scaefferi* (*Fig. 3E*), was active during two periods, early in June and in the middle of September. Cereal fields hosted high beetle catches during the sampling period, while corn fields seemed to be the least preferred habitat (*Fig. 2C, Fig. 3*).

Habitat and season

The repeated measures analysis of variance showed that there were significant differences in the activity densities and richness of ground and dung beetles caught in the seven habitats. Habitat type, season and their interaction had a significant effect on the overall number of pitfall catches (*Table 3*).



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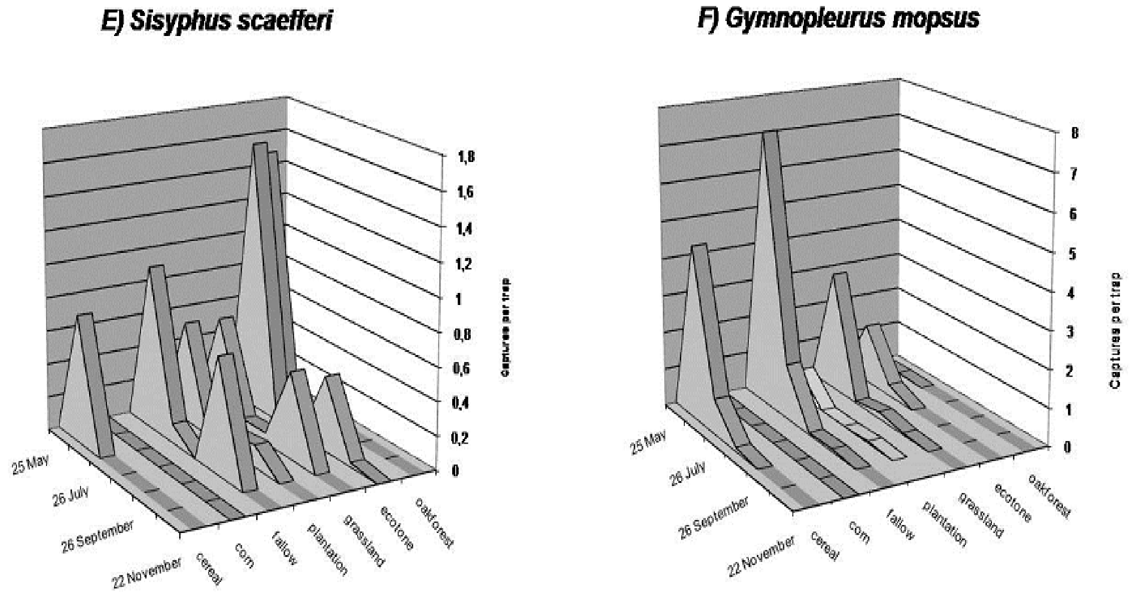

***Figure 3**. Seasonal patterns of captures of the six most abundant species: A) Onthophagus ovatus B) Onthophagus coenobita C) Pterostichus cupreus D) Pterostichus nigrita E) Sisyphus scaefferi F) Gymnopleurus mopsus*

***Table 3**. Repeated measures analysis of variance (seven monthly counts made from 25 May to 25 November) of beetles in pitfall traps suspended on seven different habitats. Results of the Tukey's b test indicate which habitat type differs significantly (p < 0.05) from the others.*

Source of variation	df	MS	F	*p*	Tukey's *b* test
Carabidae species richness					
Habitat	6	1.703	19.179	0.001	plantation>ecotone=oak forest=grassland=cereal>fallow>corn
Error	287				
Season	6	33.638	73.848	<0.001	
Habitat x Season	36	1.716	3.768	<0.001	
Error (Season)	1722	0.456			
Carabidae activity density					
Habitat	6	12.558	7.405	<0.001	plantation> grassland=cereal=ecotone=oak forest=fallow>corn
Error	287	1.695			
Season	6	204.508	22.576	<0.001	
Habitat x Season	36	38.651	4.267	<0.001	

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Error (Season)	1.722	9.059			
Scarabaeidae species richness					
Habitat	6	1.169	11.579	<0.001	fallow=grassland=cereal=ecotone>plantation> oak forest=corn
Error	36				
Season	6	29.518	49.24	<0.001	
Habitat x Season	36	2.367	3.949	<0.001	
Error (Season)	1722	0.599			
Scarabaeidae activity density					
Habitat	6	1960.13	7.148	<0.001	fallow=grassland=cereal>ecotone>plantation= oak forest=corn
Error	287	274.21			
Season	6	54336.38	36.548	<0.001	
Habitat x Season	36	7061.82	4.750	<0.001	
Error (Season)	1722	1486.72			

The inertia percentage of the correspondence analysis for the two main axes generally explained 77.32% of the species variance. The inertia percentage of the first and the second axis was 60.83% and 16.49%, respectively. Characteristic species of the cereal fields and grasslands were *O. ovatus, P. cupreus* and *P. nigrita* (*Fig. 4*) showing relative inertia 0.032, 0.035 and 0.045, respectively. *G. mopsus, S. sacer* and *O. coenobita* were proved to be characteristic species for the fallow land. Only *C. coriaceus* (Linnaeus) with relative inertia 0.050 was proven as characteristic species of corn fields, while *P. sericeus, C. nemoralis, S. scaefferi* and *M. chalybaeus* characterized ecotone and oak forest. *B. crepitans* was strongly associated with the grassland, while *Z. tenebrioides* was most abundant in the plantations.

Discussion

Seasonality of beetle assemblages

Our results indicate that: (a) an upland landscape characterized by habitat heterogeneity shaped mainly by agriculture has rich biodiversity, (b) beetle assemblages show strong seasonality, (c) characteristic species are found depending on habitat type and (d) the intermediate disturbed agricultural land uses have higher species activity densities and richness in comparison to the wooded ones.

In the present study, in an area of 138 ha, 10 dung species were collected, whereas 40 species were sampled in Northern Alps from 250,000 ha (Lumaret and Stiernet, 1989).

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Land uses in our study area and specifically open agricultural areas and grazed grasslands, generate a rather heterogeneous landscape, even at a small scale as multi fragmentation of fields characterizes it. The number of individuals of the Scarabaeidae family (15,706 adult individuals) was high although the number of species was relatively low. Regarding singletons and doubletons, 8 locally rare species were found in our study area, such as the dung beetle *Copris lunaris* (Linnaeus) and the endangered ground beetle *R. sulcatus* (Legakis and Maragou, 2009). Although recording rare species is crucial as the collective loss of rare taxa could have significant effects on ecosystem functions as well as on the services these systems provide to humans (Lyons et al., 2005), rare insect species have been scarcely studied in Mediterranean mixed forest – agricultural landscapes (Ricarte et al., 2009; Sirami et al., 2010). In our study there were only five individuals of the pest *Z. tenebrioides* collected in crop fields (wheat, 2; corn, 3) probably due to the presence of diverse perennial habitats as Miller and Jones (1997) have reported. This species is a widespread pest in the winter and spring wheat-growing areas of our study area, western and eastern Europe, western Asia, northern Africa and south-central Asia (Bonnemaison, 1980; Burnett, 1984; Borror et al., 1989; Miller, 1991; Remaudière and Remaudière, 1997), causing severe crop losses in wheat monocultures. If it is true that habitat heterogeneity affects negatively its activity densities, then it should be explored from an agronomy point of view.

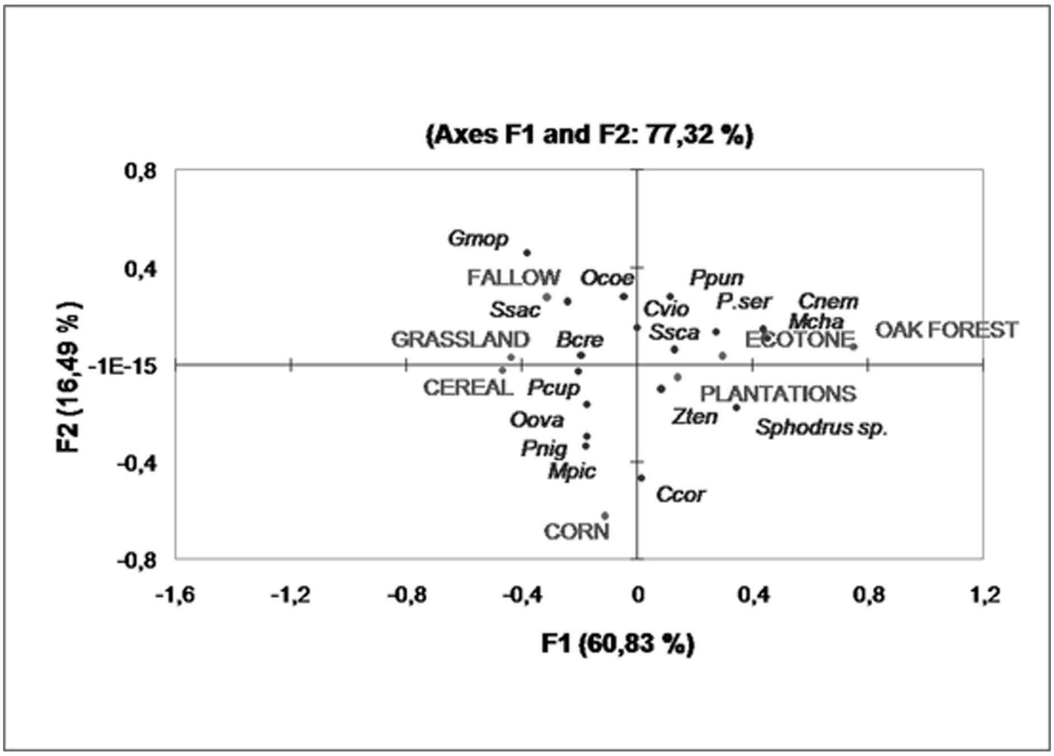

Figure 4. *Results of the correspondence analysis: spatial analysis of the species distribution among the habitats. Species names are presented with abbreviations*

Our results revealed strong seasonality, with significant differences occurring more within than between the two beetle assemblages. According to other studies, variations in community composition among different seasons are related to changes in

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temperature and humidity that affect activity (Moreno and Halffter, 2001; Romanuk and Kolasa, 2001), seasonal variability in availability of food resources and habitat productivity (Kaspari et al., 2000; Perner et al., 2005), prey availability and vegetation presence (Dennis et al., 1994). In our study, early summer samplings (i.e. June) yielded higher numbers of individuals for both assemblages than those carried out in late summer or winter. Maximum activity density in summer followed by a considerable decrease in late autumn has also been reported by Pinero and Avila (2004) and Sackmann and Flores (2009). Thiele's (1977) classic work suggested that the most frequent carabid captures occur during the season of mating and reproduction. Total activity density of individuals showed fluctuations within the main activity period of beetles (May – July) (*Fig. 2*). Given that seasonal crops such as wheat are present only for a few months possibly predatory ground beetles may serve as biological agents only during these months. When the cereals are harvested in the middle of July, the adjacent permanent vegetation, e.g. grasslands or fallow land, hosts abundant assemblages (*Fig. 3*). The presence of livestock and dung production across the study area during the summer is of paramount importance for the dung beetles resulting in the enhancement of their population (Romero-Alcaraz and Avila, 2000). In our study area, in late autumn and early winter there are no grazing animals, as the herds are moving to lower elevations, resulting in the significantly dung decrease and probably may affect dung beetle population.

Our results pointed out that habitat heterogeneity had a positive effect on alpha diversity of beetles, with significant variations among seasons. Our results demonstrated that habitat type affected the diversity parameters examined for beetle assemblages, while specific species characterized cereal fields, grasslands, ecotone and oak forest according to the correspondence analysis. Specifically, grasslands and fallow land had higher activity density and species richness of both assemblages in comparison to oak forest. Similarly to our study, Wassmer (1995) showed that population densities of dung beetles were higher in open areas, like pastures, than in the wooded areas, whereas da Silva et al. (2008) reached the same conclusion for ground beetles in Portugal. It has also been suggested that carabids dominate the most exposed habitats like agricultural areas, where they usually find high food availability, caused by the heterogeneity of vegetation (Niemelä, 1997), due to their high mobility and invasive ability (Larsen et al., 2003). The low carabid richness of the forest probably suggests that fewer species are adapted to relatively cool and dark forest habitats (Niemelä, 1993). In our heterogeneous landscape, crops are the most disturbed habitat, due to the complete removal of crop biomass at harvest. Forest is the least affected habitat by the removal of plant biomass in terms of timber; fallow land, plantations and grasslands can be considered intermediate disturbed habitats, falling between crops and forest, as in the latter the vegetation cover is almost permanent, and frequently reduced due to the livestock grazing. The existence of habitat diversity favors the coexistence of species in the area that have different habitat preferences, leading to effective spatial separation of them (Giller and Doube, 1994). On the contrary, some widely distributed species, such as *O. coenobita*, have shown high plasticity in habitat preference across different geographical areas, illustrating possible effects of climatic factors (Lumaret and Kirk, 1987; Wassmer, 1995).

Livestock raising and extensive agriculture should be carried out in such mountainous areas and are strongly recommended in similar landscapes as they have positive effects on the beetle fauna. Similar future studies on the effects of habitat types

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and elements configuration in different spatial and seasonal scales on the beetle fauna, leading to targeted agricultural applications, should be implemented. In addition, biotic factors such as the abundance of predators or prey should be explored to explain habitat heterogeneity – species diversity relationships.

In conclusion, in this upland heterogeneous Mediterranean landscape, significant differences in beetle richness and activity densities were revealed among different seasons and habitats. A striking outcome is that agriculture, which creates habitat heterogeneity in the landscape context, has rather positive effects on beetle diversity. It is also demonstrated that less disturbed habitats, such as the young oak forest in our study area, do not favor diversity. Another apparent outcome is that the estimated non parametric indices performed well comparing to the observed richness, suggesting that they could be used in biodiversity surveys avoiding cost-effective protocols.

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ADDITIONAL WEB RESOURCES

http://purl.oclc.org/estimates/
www.iucn.org/redlist/
http://www.xlstat.com

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