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Ground beetles respond to grazing at assemblage level, rather than species-specifically: the case of Cretan shrublands

Dimitris Kaltsas · Apostolos Trichas · Kostas Kougioumoutzis · Maria Chatzaki

Abstract Phrygana, maquis and subalpine shrublands are the most typical ecosystem types on the island of Crete. However, these formations are mostly mismanaged and poorly studied in terms of their fauna and the effect of long term land-use. We studied the impact of goat and sheep grazing on the diversity patterns of carabid beetles at 40 sites in relation to possible habitat uniqueness and geographic zonation. In total, 19,322 individuals belonging to 42 Carabidae species were identified. The composition of site assemblages was mainly determined by altitude. The six Cretan endemic species collected were widely distributed on the island and most of them were dominant. Species richness and equitability were significantly lower at overgrazed sites compared to areas with low grazing intensity. The diversity patterns of carabids were influenced by the level of grazing in each study area. As species richness and diversity were maximal under moderate/relatively high levels of grazing (hump-shaped pattern), our results support the intermediate disturbance hypothesis. Low tolerance of carabid taxa to intensive grazing was also ascertained through the significantly high values of temporal beta diversity at overgrazed sites, independent of local species richness. We conclude that Carabidae are good indicators of grazing pressure in Crete at assemblage level, rather than species-specifically. To maintain diversity and enhance niche space of invertebrate fauna, the spatiotemporal discontinuity of grazing is essential.

Introduction

The lowland eastern Mediterranean landscape is characterized by the dominance of drought-deciduous shrubs, known as phrygana (sensu di Castri 1981). As altitude increases, this low and thorny vegetation is gradually replaced by maquis, which consist of evergreen taller shrubs or small trees and occur as the environment becomes wetter (Margaris 1981). However, these two vegetation types are often intermixed, the limits between the two being vague (Rackham and Moody 1996). This mosaic vegetation is often related to irregularities in soil and bedrock, to the clonal growth of maquis dominants or to overgrazing (Vogiatzakis and Rackham 2008). Many of these species grow hard, thorny and distasteful leaves, as a response to grazing pressure (Margaris and Koutsidou 2002). Nevertheless, overgrazing, agricultural intensification or abandonment, fire, as well as episodic droughts due to the progressively increased aridity, have increased vegetation fragility (Le Houérou 1981). Consequently, degradation increased during the historical epoch (di Castri et al. 1981), which is primarily visible through the reversal in succession (Tzanopoulos et al. 2007) and/or an increase in ruderal species (Calaciura and Spinelli 2008).

D. Kaltsas (✉) · A. Trichas
Natural History Museum of Crete, University of Crete, Knossos Av., P.O. Box 2208, 71409 Irakleio, Crete, Greece
e-mail: dimitris.kaltsas@gmail.com; dimitris@nhmc.uoc.gr

K. Kougioumoutzis
Division of Plant Biology, Department of Biology, University of Patras, Rion, 26500 Patras, Greece

M. Chatzaki
Department of Molecular Biology and Genetics, Democritus University of Thrace, Dragana, 68100 Alexandroupolis, Greece

Phrygana, maquis, their mosaic-like formations and subalpine shrubs cover more than half of the area of Crete, the fifth largest island in the Mediterranean. Crete has been called a "miniature continent", due to its long isolation history and the intense tectonic dynamics of the area (Rackham and Moody 1996). Though shrublands are usually present at low elevations, they may reach the alpine zone, confirming the weak zonation of vegetation on Crete (Vogiatzakis and Rackham 2008). Grazing is one of the oldest human activities on the island, common all over Crete during the last centuries. Despite the high priority level of several phryganic and maquis biotopes for conservation and management (Dimopoulos et al. 2006), these patches of indigenous Mediterranean-type vegetation remain marginalized from conservation practice.

The possible effects of long-term land use on animal abundance and diversity in the Eastern Mediterranean region have been overlooked and poorly studied, especially in terms of arthropod assemblages (Kaltsas et al. 2012), which have widely proved to be an ideal group at assessing the ecological impacts of land use and disturbance (Eyre et al. 1986). Carabidae, the largest family of Adephaga Coleoptera, is among the main reasons for the established importance of insects in conservation biology (New 2010). Their occurrence in all terrestrial habitats, their relatively well known taxonomy, the morphological variability, life history and ecological requirements of carabid taxa, and the fact that they are easily captured by pitfall trapping, have arguably made Carabidae excellent model organisms for research on conservation ecology (New 2010; Kotze et al. 2011).

Previous studies have shown that habitat type is an important explanatory factor of carabid community composition (Jeanneret et al. 2003; Aviron et al. 2005). The diversity of carabids has been proved to be highest in coastal and inland shrublands of Crete, with the local endemic taxa being the most abundant species at all habitat types (Trichas 1996). Additionally, the life history of carabids may change with altitude, as an adaptive ability to temperature change (Butterfield 1996). Ground beetle communities show measurable responses to various human activities, especially concerning agricultural practices, forestry, and grazing regimes (Kotze et al. 2011 and references therein), and are considered as useful bioindicators of habitat alteration (Rainio and Niemelä 2003). Specifically, grazing intensity influences carabid distribution and assemblage composition through changes in the (a)biotic environment (McFerran et al. 1994; Dennis et al. 1997; Moran et al. 2012). Consequently, large brachypterous species with poor dispersal abilities are least abundant or absent under intensive grazing (Blake et al. 1996; Ribera et al. 2001; Cole et al. 2006).

Contrary to the numerous studies on carabids for evaluating the impact of human activities in northern temperate regions, the distributional and diversity patterns of ground beetles in relation to land-use in SE Mediterranean are largely unknown. The objective of this study was to investigate the impact of grazing intensity on the spatio-temporal diversity patterns of carabids in relation to possible habitat uniqueness and geographic zonation of ground beetle species in shrublands of Crete. The following hypotheses were tested: (1) species richness, abundance and diversity of carabids are lowest under severe disturbance (overgrazing), (2) species richness is lowest at very high altitudes, (3) the carabid assemblage composition changes in different habitat types. The ultimate goal of our
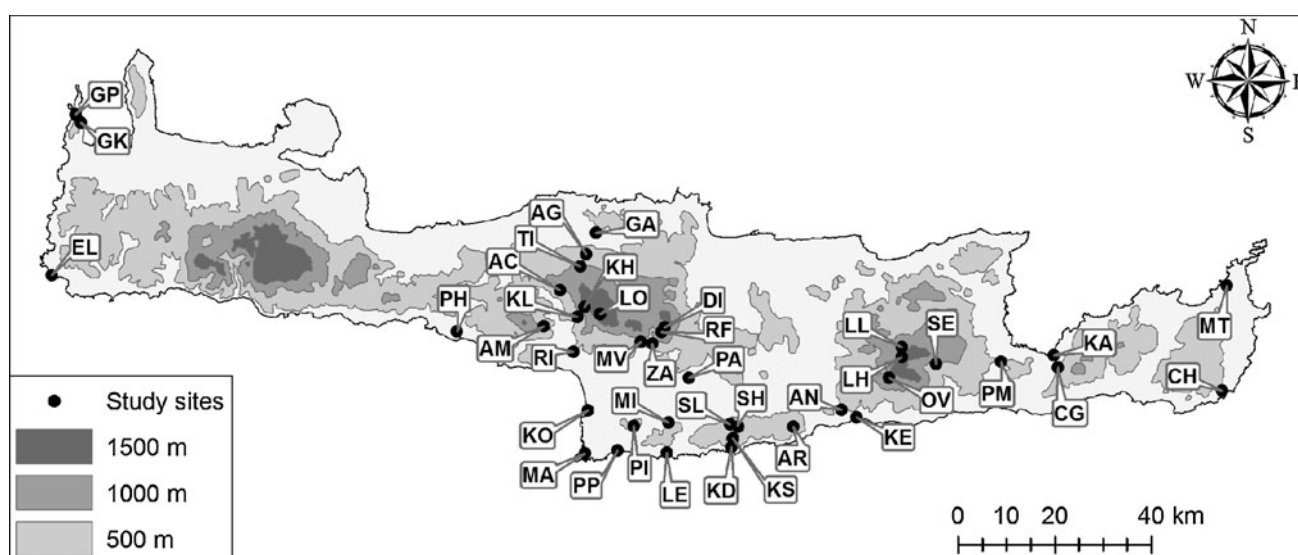

Fig. 1 Localities of the 40 sampling sites in Crete. Study site characteristics in Appendix 1

study was to test the suitability of Carabidae species as indicators of grazing pressure on the island.

Materials and methods

Study sites

Specimens were collected at 40 study sites (Fig. 1). The specific sites were selected to cover all the grazing levels at Cretan shrublands, within their geographic range in the island. Thus, sampling was conducted from the north-western end (Gramvousa) to the southeastern end of Crete (Chamaitoulo), and from almost sea level near the southern coasts of the island up to high elevations in Psiloritis and Dikti mountains, under all current grazing regimes in Crete. All sites were located within areas with natural phryganic, maquis or subalpine shrub vegetation. The dominant phryganic species at low elevations are: *Sarcopoterium spinosum*, *Thymbra capitata*, *Genista acanthoclada*, *Calicotome villosa*, *Phlomis lanata*, *Phlomis fruticosa*, *Cistus creticus*, *Cistus salviifolius*, *Euphorbia acanthothamnos* and *Ballota pseudodictamnus*. The arborescent maquis species which dominate mainly at intermediate altitudes are *Pistacia lentiscus*, *Juniperus phoenicea*, *Quercus coccifera*, *Arbutus unedo*, *Ceratonia siliqua* and *Euphorbia dendroides*. At higher altitudes subalpine shrubs include *Berberis cretica*, *Rhamnus saxatilis* and *Astragalus angustifolius*.

We grouped the study sites into four altitudinal zones, based on the altitudinal arrangements proposed by Quézel and Barbero (1982) for the Mediterranean region and made slight adjustments regarding the timberline in Crete (Trichas 1996; Lymberakis 2003): ALT1 (0–399 m)—thermo-mediterranean zone, ALT2 (400–699 m)—meso-mediterranean zone, ALT3 (700–1,599 m)—supra-mediterranean zone, and ALT4 (1,600–2,199 m)—montane mediterranean zone. Four different habitat types were distinguished: coastal phrygana (CP), inland phrygana (IP), maquis (M) and sub-alpine shrubs (SS), following Chatzaki et al. (2005). In cases of mosaic vegetation, the habitat characterization was decided by the cover of dominant species (Appendix 1). Even though longitudinal patterns are usually not detected in relatively small areas such as Crete, the longitude of sampling sites was also included in our study as a predictor variable, due to the climatic and faunal variation from east to west Crete (Legakis and Kypriotakis 1994).

The number of grazing animals in a given area is usually used as a disturbance or degradation metric (New 2010). However, there are no reliable data regarding the exact or even the average number of grazing animals in Crete (Rackham and Moody 1996). Hence, we used another standard estimation procedure of habitat degradation which

has been applied in conservation ecology (Paschetta et al. 2012). Several plant taxa are indicator species for a variety of environmental factors, as well as for grazing (Ellenberg 1952; Ellenberg et al. 1992; Böhling et al. 2004; Höft et al. 2010). *Asphodelus aestivus*, *Drimia maritima*, *Phlomis cretica*, *P. fruticosa*, *P. lanata* and *Onopordum* spp. are considered as good grazing indicators in Greece (Horvat et al. 1974; Papanastasis and Noitsakis 1992). Thus, their level of coverage and dominance was measured using the Braun-Blanquet method with a plot size of 100 m^2 at each site, as suggested for shrublands (Braun-Blanquet 1964). The level of grazing at each site was determined as the average cover of indicator plant species. Accordingly, we set six theoretical classes of grazing disturbance: G0—no grazing (<1 % coverage of the study site by grazing indicators), G1—occasional/rare grazing (1–5 % coverage), G2—low grazing intensity (5–25 % coverage), G3—intermediate grazing (25–50 % coverage), G4—intense grazing (50–75 % coverage), G5—overgrazing/degradation due to grazing (75–100 % coverage). No sites were grouped into G0 and G1 classes (Appendix 1), because relatively or generally ungrazed areas are very scarce in Crete.

Sampling and taxonomic identification

Samples were collected using pitfall traps (plastic containers 12 cm tall, 9.5 cm diameter at the top), containing ethylene glycol as preservative and placed flush with the ground surface. Pitfall traps were set at the centre of shrubland formations, in order to avoid the edge effect (Magura 2002). The 15–20 traps were set along a transect line at every site (inter-trap distance: 10–20 m) and were changed at 2 months intervals. Sampling lasted for 1 year at all study sites and took place between the summer of 1996 and the summer of 2001 (Appendix 1). Samples were sorted and all Carabidae specimens were identified to species level. Nomenclature follows Löbl and Smetana (2003) and taxonomic changes thereafter. The material is deposited in the Coleoptera collection of the Natural History Museum of the University of Crete.

Data analysis

Species richness for each study site was estimated using three common nonparametric, incidence-based estimators that calculate species-by-sample data: Chao1, Jacknife1 and Bootstrap (detailed description in Colwell 2009). Sampling completeness was estimated as the average estimated richness divided by the number of collected species. We set a minimum of 75 % as the lower limit of sampling completeness (Meijer et al. 2011). To ensure that the local inventories could be considered as an adequate description of their richness, we also tested the asymptotic

level of the respective accumulation curves, by measuring the slope between the last two points of each curve (Hortal and Lobo 2005). Preliminary results showed that the asymptote values became regular at a slope value of 0.04, so we set this score as the down threshold of sampling adequacy. Richness estimations and accumulation curve data were produced in EstimateS 8.2.0, based on the mean of 50 randomizations (Colwell 2009), setting the number of individuals as a surrogate for the sampling effort. Undersampled sites were excluded from all diversity analyses.

To determine whether the study sites differed in their composition and activity density of species (number of individuals/100 trap-days) in relation to an ecological (habitat, grazing level), temporal (year of study) or geographical factor (altitude, longitude), we applied Analysis of Similarities (ANOSIM) with 9,999 permutations. Common and rare species were equally weighted with square root transformation of data. Correlation between categorical factors (habitat, grazing level, year, altitude, longitude) was detected using Cramer's V coefficient. SIMPER analysis was used to determine which species contributed most to the average Bray–Curtis dissimilarity between factor classes in ANOSIM in PAST 2.15 (Hammer et al. 2001). The activity densities of species in different factor classes were compared using one-way ANOVA. The differences among carabid site assemblages in different factor classes were visualized with non-metric multidimensional scaling (NMDS). To classify the 40 site assemblages, we applied cluster analysis using the flexible beta ($\beta = -0.25$) linkage method with the Bray–Curtis distance measure. The cluster dendrogram was pruned according to objective criteria provided by indicator species analysis, which combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group (Dufrêne and Legendre 1997). Specifically, we chose the number of clusters with the lowest average P value and highest number of significant indicators. Statistical significance was tested compared to the average of 4,999 permutations. Indicator species analysis was also applied to test for potential grazing indicators, setting the level of grazing as the grouping variable. We performed the analysis in total, and on community level, i.e. separately for each clade of the cluster dendrogram, in order to avoid the possible overriding effect of other factors (e.g. altitude, habitat, longitude). We excluded all species represented by 1–20 individuals in the raw data (Pohl et al. 2007). The maximum value of IndVal is 100, when all individuals of a species are solely captured at all sites of one specific factor class. NMDS, cluster analysis and indicator species analysis were performed in PC-ORD 6.04 (McCune and Mefford 2011).

The diversity of carabids at each site was measured through Simpson's diversity index (D) which is a measure of equitability, and the Shannon index (H') (details in Magurran 1988). Both indices were used for paired-sites comparisons using a permutation test with 1,000 random matrices including two columns, each with the same row and column totals as in the original data matrix. A small P value indicates a significant difference in diversity index between the two site assemblages. Diversity estimations and pairwise comparisons were performed in PAST 2.15 (Hammer et al. 2001).

The temporal dynamics of local assemblages were analysed on the basis of $\bar{\alpha}$ diversity (average number of species per sampling period, i.e. 2 months) and the proportion of cumulative α diversity:

$$\alpha\% = (\bar{\alpha}/S) \times 100$$

(S: total number of species collected in a site) (Zamora et al. 2007), which is a measure of temporal turnover (Romanuk and Kolasa 2001). Temporal beta diversity (βt) was measured as the temporal change of site assemblage structure. We applied the complementarity index of Colwell and Coddington (1994):

$$C_{jk} = \left[(S_j + S_k - 2V_{jk}) / (S_j + S_k - V_{jk}) \right] \times 100$$

where S_j is the number of species captured in sampling period j, S_k the number of species captured in consecutive sampling period k ($k = j + 1$) and V_{jk} the common species captured in periods j and k. C_{jk} was calculated for consecutive sampling periods and βt was calculated as average for each site assemblage. We tested if temporal beta diversity (βt) decreases as $\alpha\%$ increases using a simple linear regression.

The potential determinant role of an ecological/geographical factor to the species richness, diversity (D, H'), and temporal diversity ($\bar{\alpha}$, $\alpha\%$, βt) was investigated using multiple regression analysis to reveal a possible monotonous decrease/increase of variables with each factor. In cases of non-significance, polynomial regression was used to test for non-linear relations, such as hump-shaped patterns. The year of study was highly correlated with altitude (Spearman's $r_s = 0.372$; $P = 0.018$) and longitude (Spearman's $r_s = 0.434$; $P = 0.005$), whereas there was no significant bivariate correlation between the other predictors (longitude, altitude and grazing) ($-0.23 <$ Spearman's $r_s < 0.07$, $P > 0.05$). In order to avoid collinearity of factors, we excluded year of study from regression analysis. The variance of richness and diversity among different years of study and habitat types was tested using one-way ANOVA. The local assemblages were classified in accordance to the six variables (S, D, H', $\bar{\alpha}$, $\alpha\%$, βt) in a biplot using principal components analysis (PCA). All variables were normalized prior to analysis using division by their

standard deviations, due to the different units of measurement among variables (Hammer et al. 2001). We considered principal components (PCs) with eigenvalues >1.

Results

Composition of carabid assemblages

We identified 26 genera (7.6 ± 2.5 per site) and 42 Carabidae species (8.2 ± 3 per site) in a total of 19,322 individuals (1,665.6 ind./100 trap-days) for the 40 sites (Appendix 2). The average species-genus ratio was very low (1.07 ± 0.09 per site) (Table 1). Ten species were singletons (represented by single individuals). The six Cretan endemic species were among the 11 most abundant species, comprising 33 % of the total activity density. *Calathus fuscipes* was the most abundant species (698.04 ind./100 trap-days), followed by *Cymindis lineata* (276.7 ind./100 trap-days) and Cretan endemic *Carabus banoni* (262.12 ind./100 trap-days), which was captured at all sites, except one (KE). The second most widely distributed species was *Cymindis lineata* (26 sites). Cretan endemic species were present at 21.17 ± 10.15 sites on average, whereas non-endemic species were much more narrowly distributed (5.39 ± 6.57 sites). Sampling proved inadequate for 11 sites, five of which were G5 sites (Table 1).

Cramer's *V* coefficient showed that altitudinal zones were significantly correlated with habitat types ($V = 0.583$; $P < 0.001$) and year of study ($V = 0.46$; $P = 0.01$), mainly due to the altitudinal character of subalpine shrublands and the fact that samplings at all ALT4 sites were conducted at the same year (Appendix 1). ANOSIM showed that altitude was the most influential factor for the composition of carabid site assemblages, followed by year of study and habitat type which were also significant. Specifically, the species composition of local assemblages differed significantly across the four altitudinal zones. The only lack of variation was between the lowest altitude zones (ALT1–ALT2, $R = 0.115$, $P = 0.139$). On the contrary, longitude proved to have no effect on local assemblage composition, whereas grazing level was marginally insignificant ($P = 0.078$), but with a low R statistic ($R = 0.062$) (Table 2). Site assemblages at phryganic (CP, IP) and maquis (M) habitats were similar among each other ($-0.089 < R < 0.136$; $0.091 < P < 0.731$) and were significantly different than in subalpine shrubland (SS) sites ($0.431 < R < 0.558$; $0.006 < P < 0.029$). Similarly, only site assemblages during the year of sampling at SS (ALT4) sites differed with other years of study ($0.329 < R < 0.34$; $0.018 < P < 0.023$), confirming this altitudinal pattern. SIMPER analysis showed that eight species contributed to this zonation of carabid fauna (Table 3). These were: *Cymindis lineata*, *Calathus*

Table 1 Species richness estimation results for the 40 sites (arranged by increasing grazing intensity, G2–G5)

Site Code	Grazing level	S	S/G	Singletons (%)	Sampling completeness (%)	Slope
GA	G2	6	1	20	93.56	0.004
KA	G2	7	1	28.57	82.06	0.018
KD	G2	7	1.167	28.57	82.84	0.019
KS	G2	7	1.167	0	94.17	0.003
LH	G2	5	1	0	99.14	0
PM	G2	5	1	0	92.03	0.004
SH	G2	7	1	28.57	81.24	0.003
AG	G3	10	1.111	20	84.22	0.02
AM	G3	7	1.167	14.29	94.21	0.001
CG	G3	6	1	16.67	88.11	0.012
GK	G3	9	1.125	11.11	87.91	0.008
KH	G3	13	1.083	0	94.09	0.001
LL	G3	8	1	25	89.49	0.008
LO	G3	9	1	22.22	88.5	0.003
MA	G3	6	1	0	92.83	0.004
MI	G3	11	1.222	36.36	76.21	**0.046**
MT	G3	8	1	0	94.3	0.003
MV	G3	11	1	36.36	77.14	**0.058**
PI	G3	9	1.125	22.22	80.31	0.015
AC	G4	8	1.143	25	87.4	0.008
AN	G4	10	1	10	83.06	0.027
AR	G4	11	1.1	9.09	91.97	0.019
DI	G4	10	1	30	82.92	0.005
EL	G4	7	1.143	37.5	78.07	0.039
KL	G4	8	1.143	12.5	86.15	**0.047**
OV	G4	12	1.2	33.33	77.82	0
PP	G4	6	1	33.33	85.56	**0.059**
RF	G4	15	1.153	20	81.73	0.009
RI	G4	5	1.25	20	76.26	**0.049**
SE	G4	16	1.23	37.5	**69.78**	**0.043**
TI	G4	14	1.272	0	89.51	0.002
CH	G5	5	1	40	77.32	0.039
GP	G5	10	1	40	**74.46**	0.027
KE	G5	4	1	50	79.89	**0.132**
KO	G5	7	1	57.14	**65.85**	0.036
LE	G5	6	1	33.33	82.65	0.039
PA	G5	7	1	57.14	**66.6**	**0.05**
PH	G5	7	1	57.14	**74.07**	**0.073**
SL	G5	5	1	0	91.3	0.023
ZA	G5	3	1	0	97.93	0

S, number of species; *S/G*, species-genus ratio; Singletons (%), percentage of species represented by a single individual; Sampling completeness %, average proportion of the number of species expected, i.e. the average estimation of Chao1, Jacknife1 and Bootstrap divided by *S*; Values <75 % are highlighted; Slope, the final slope of each accumulation curve; Values ≥0.04 are highlighted; Undersampled site assemblages are also highlighted

Table 2 ANOSIM results: R statistic, percentage of significance of pairwise tests among classes of each factor and P values (significant values highlighted)

	R statistic	% Significance	P
Longitude	−0.018	0	0.588
Altitude	0.434	83.33	**<0.001**
Habitat	0.182	50.00	**0.021**
Grazing	0.062	20.00	0.078
Year	0.209	33.33	**0.019**

fuscipes and *Calathus oertzeni* which were mostly abundant in ALT3 zone, *Zabrus oertzeni*, *Harpalus honestus*, *Calosoma inquisitor* and *Acinopus picipes* which were typical at very high elevations (ALT4, SS) and *Carabus banoni* which was much more abundant at low altitudes.

The altitudinal zonation of sites is apparent in the two-dimensional NMDS ordination plot, that explained 68.6 % of the variance in the distance matrix (Axis 1: 46.4 % of variance, Axis 2: 22.2 % of variance, stress = 0.20; Fig. 2). The cluster dendrogram of local assemblages is presented in Fig. 3. Based on the results on indicator species analysis (Table 4), the 40 sites were classified into five clades, two of which included the two sites (KE, LO) which were ouliers in the NMDS plot (Fig. 2). Clusters C1–C3 (Fig. 3) represent the three broad carabid communities. C1 and C2 mainly consist of sites at ALT1 and ALT2 zones, whereas C3 solely includes ALT3 and ALT4 sites.

Though ANOSIM showed that grazing was not a determinant factor for the composition of carabid local assemblages (Table 2), carabid composition in G2 and G5 sites proved to be significantly dissimilar ($R = 0.167$, $P = 0.045$), mainly due to *Carabus banoni* and *Cymindis lineata* (SIMPER % contribution: 16.57 and 14.35 respectively). One-way ANOVA showed that the average abundance of *Carabus banoni* and *Cymindis lineata* in G5 sites was significantly lower than in G2 sites ($9.732 < F < 11.156$;

$0.005 < P < 0.008$). Indicator species analysis with grazing as the grouping factor performed in total and separately for community C1 (Fig. 3) did not reveal any significant carabid indicator species. However, *Platyderus jedlickai* proved to be a significant indicator at G4 sites in communities C2 and C3 (C2: IndVal = 68.5, $P = 0.037$; C3: IndVal = 88.4, $P = 0.004$).

Spatiotemporal diversity patterns

Despite the overriding effect of altitude on the composition of local assemblages, the variation of carabid diversity on Crete was mainly influenced by grazing intensity. Multiple regression showed that none of the dependent variables were influenced by longitude and altitude, whereas temporal turnover (α %) and temporal diversity (βt) were influenced by the grazing level at the study sites (Table 5). The temporal beta diversity of carabids (βt) decreased as the cumulative temporal α diversity (α %) increased [regression model: $\beta t = 90.42 - 0.67(\alpha$ %$)$, $r^2 = 0.448$, $P < 0.001$], while both measures (α %, βt) were independent of species richness ($0.041 <$ Spearman's $r_s < 0.109$, $P > 0.05$). One-way ANOVA showed that no variables varied significantly among different habitat types ($0.663 < F < 3.611$; $0.057 < P < 0.79$) and years of study ($0.064 < F < 0.958$; $0.423 < P < 0.978$). Thus, the richness and diversity patterns at site level were solely determined by grazing intensity.

The total and average temporal richness (S, $\bar{\alpha}$), as well as the general diversity measures (H', D) followed a significant hump-shaped pattern with grazing intensity (Table 5), peaking at intermediate disturbance levels (Fig. 4a–d). Temporal diversity (α %) increased as grazing intensity decreased (Fig. 4e) while the temporal change of site assemblage structure (βt) increased with grazing intensity (Fig. 4f), denoting the different phenological patterns of co-occurrent carabid species at G5 sites, as a result of mutual avoidance. The highest values of βt were measured

Table 3 SIMPER analysis results

	ALT1–ALT3	ALT1–ALT4	ALT2–ALT3	ALT2–ALT4	ALT3–ALT4
Av. dissimilartiy	70.59	79.35	67.76	75.98	67.00
R statistic	0.590	0.749	0.515	0.707	0.421
P	<0.001	0.002	<0.001	0.011	0.037
Acinopus picipes		12.34		12.74	10.97
Calathus fuscipes	20.12		20.43		15.09
Calathus oertzeni	10.04		10.37		7.52
Calosoma inquisitor		7.27			
Carabus banoni	7.17	6.65	8.05	7.63	
Cymindis lineata	13.02	16.45	12.85	16.19	14.73
Harpalus honestus		12.77		13.15	10.24
Zabrus oertzeni	12.75	8.41	12.22	7.65	6.88

The species with highest contribution (%) to the significant differences of sites between altitudinal zones (details in Fig. 2). ANOSIM results on the average dissimilarity and significance of differences between pairs of altitudinal zones are also reported
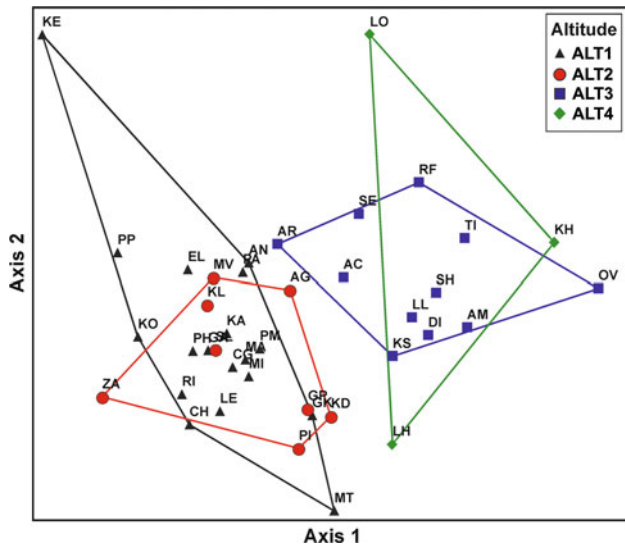
Fig. 2 2D NMDS ordination plot based on the Bray–Curtis dissimilarity matrix of the 40 carabid site assemblages among the four altitudinal zones. ALT1: 0–399 m, ALT2: 400–699 m, ALT3: 700–1,599 m, ALT4: 1,600–2,199 m

Table 4 Indicator species analysis results on the number of clades in the cluster dendrogram (Fig. 3)

No. of clusters	Sig. indicators	Av. *P*
2	12	0.4209
3	12	0.4195
4	13	0.4186
5	**14**	**0.4183**
6	13	0.419
7	13	0.4189

The maximum number of indicators and the minimum average *P* value are highlighted

for carabids at G5 sites (CH, LE, SL, ZA), as well as two G4 sites (EL, AR).

The first three principal components with eigenvalues >1 accounted for 94.483 % of the total variation (Table 6). Temporal beta diversity βt, (negative), Shannon H', Simpson D and temporal diversity $\bar{\alpha}$ (positive) provided the highest loadings on PC1, which accounted for 53.797 % of the total variance. The proportion of cumulative α diversity α % (negative) and βt (positive) showed the highest loadings on PC2 (Table 6). The PC1–PC2 biplot (Fig. 5a) showed that carabids at G5 sites with low diversity and high βt were clearly separated from all other local assemblages by PC1. Carabids at G2 (high α %) and G5 sites (high βt) were separated by PC2. The PC1–PC3 biplot (Fig. 5b) showed the distinctiveness of site assemblages at G5 sites, whereas all others were very closely ordinated. As shown by the convex hulls in Fig. 5, the diversity patterns of ground beetles at intermediate-high grazing levels (G3, G4) varied highly compared to the respective patterns at G2 and G5 sites. Indeed, permutation test comparisons showed that both measures of diversity (H', D) of ground beetles in G2 and G5 sites differed most with G3 and G4 sites respectively, whereas both diversity measures were highly variant among carabids in G4 sites, as well in G3 sites, contrary to G2 and G5 grazing classes (Table 7).

Fig. 3 Cluster dendrogram of the 40 study sites based on the activity density of carabid species using the the flexible beta ($\beta = -0.25$) linkage method with the Bray–Curtis distance measure. The *dashed line* indicates the pruning level based on the results of indicator species analysis (Table 4). Clusters C1–C3 represent the three broad carabid communities, which were further analyzed
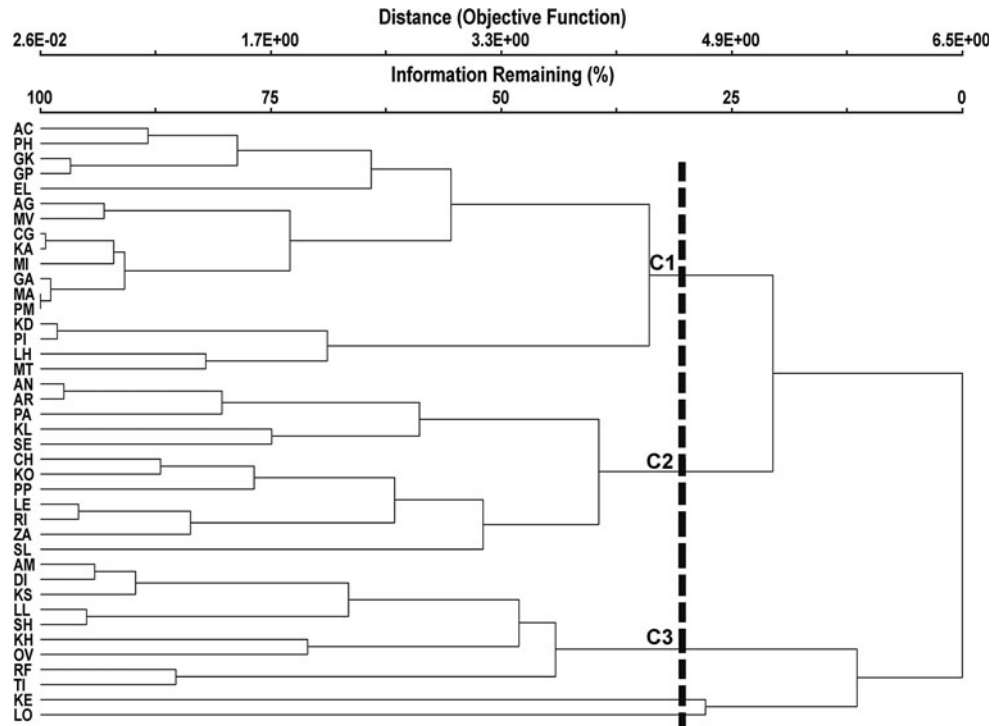
Discussion

Our findings indicate that grazing intensity significantly influenced the species richness and diversity patterns of carabids in shrublands of Crete. Even though altitude was the main determinant factor for the composition of local assemblages, there was no significant pattern of species richness with altitude, contrary to our initial hypothesis. The only habitat specialization of ground beetles revealed was for subalpine shrublands (above 1,600 m), confirming the altudinal zonation of ground beetles on Crete. The average diversity was minimal at overgrazed sites and followed a hump-shaped pattern with grazing intensity.

Composition of local assemblages

The composition of carabid site assemblages was mainly determined by altitude (Table 2), indicating the predominant role of biogeographic processes over longitude and disturbance level. The carabid fauna in shrublands of Crete was characterized by: 1) lowland species, rare in high altitudes, such as *Carabus banoni*, 2) widespread species on the island, mostly abundant in the intermediate altitudinal zone (e.g. *Cymindis lineata*, *Calathus fuscipes*, *Calathus oertzeni*), and 3) species exclusively present (*Harpalus honestus*, *Acinopus picipes*, *Calosoma inquisitor*) or generally common at high altitudes (*Zabrus oertzeni*)

Table 5 Multiple regression results on the influence of non-collinear environmental factors (predictor variables) on species richness, sampling completeness/adequacy and diversity measures on classes

	Multiple linear regression					Polynomial regression		
	b	SE	t	*P*	r^2	F	*P*	r^2
S								
Constant	27.059	27.539	0.983	0.062				
Longitude	−0.834	1.082	−0.771	0.446	0.018			
Altitude	0.002	0.001	1.883	0.068	0.067			
Grazing	0.617	0.625	0.987	0.33	0.013	5.82	**0.006**	0.239
Shannon *H′*								
Constant	1.608	0.309	5.212	0.000				
Longitude	−0.125	0.066	−1.883	0.071	0.140			
Altitude	0.074	0.052	1.422	0.167	0.108			
Grazing	−0.060	0.055	−1.097	0.283	0.042	5.684	**0.009**	0.304
Simpson *D*								
Constant	0.777	0.140	5.534	0.000				
Longitude	−0.053	0.030	−1.761	0.090	0.123			
Altitude	0.034	0.024	1.449	0.160	0.111			
Grazing	−0.035	0.025	−1.415	0.169	0.068	3.757	**0.037**	0.224
$\bar{\alpha}$								
Constant	4.740	1.423	3.331	0.002				
Longitude	−0.136	0.287	−0.473	0.639	0.002			
Altitude	0.405	0.237	1.704	0.097	0.108			
Grazing	−0.392	0.237	−1.650	0.108	0.096	14.66	**< 0.001**	0.442
α %								
Constant	11.432	59.601	0.192	0.085				
Longitude	1.958	2.341	0.836	0.408	0.051			
Altitude	0.004	0.003	1.667	0.102	0.122			
Grazing	−6.03	1.353	−4.457	**< 0.001**	0.408			
*β*t								
Constant	46.992	7.751	6.063	0.000				
Longitude	−1.869	1.565	−1.194	0.240	0.052			
Altitude	−1.491	1.293	−1.153	0.256	0.078			
Grazing	7.011	1.293	5.421	**< 0.001**	0.490			

In cases of non-significance, polynomial regressions were fitted. All significant polynomial regression results refer to 2nd order equations. *S*, species richness; $\bar{\alpha}$, average number of species per sampling period; α %, ($\bar{\alpha}$/S) × 100; *β*t, complementarity index (Colwell and Coddington 1994)
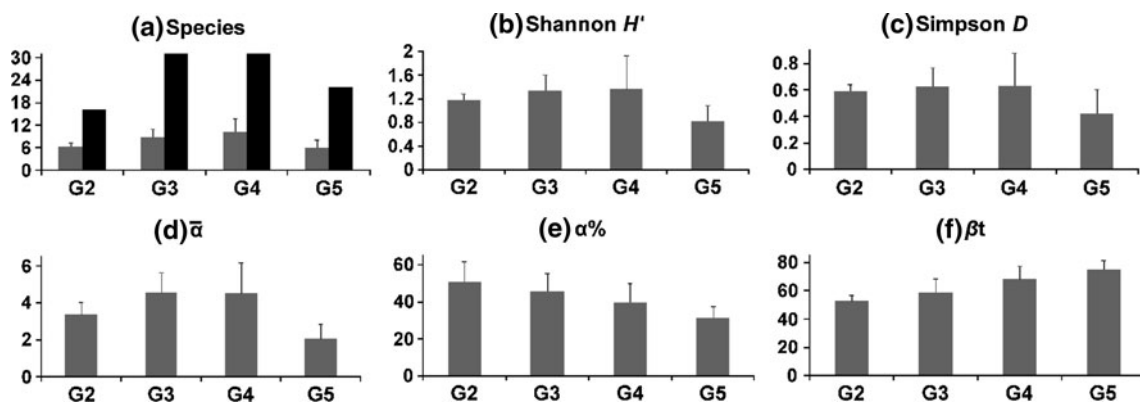
Fig. 4 Average ± SD of **a** species richness, *S*, **b** Shannon *H'*, **c** Simpson *D*, **d** average number of species per sampling period, ᾱ, **e** proportion of cumulative temporal α diversity, α %, and **f** temporal beta diversity, *β*t of carabid site assemblages under G2–G5 grazing regimes. *Black bars* total number of species at each grazing level

Table 6 PCA results on six diversity variables measured for each adequately sampled local assemblage

	PC1	PC2	PC3
Eigenvalue	3.228	1.338	1.103
% variance explained	53.797	22.308	18.378
Variables	Factor loadings		
S	0.3698	0.3358	−0.5635
ᾱ	0.4255	0.1157	−0.4740
α %	0.4070	−0.5223	−0.1086
*β*t	−0.3154	0.6665	0.0829
Shannon *H'*	0.4609	0.3242	0.3722
Simpson *D*	0.4254	0.2277	0.5483

PCs with eigenvalues >1 are included. *S*, ᾱ, α %, *β*t as explained in Table 5

(Table 3, Appendix 2), replacing congeneric lowland species (*Z. graecus*) (Trichas 1996). Previous studies showed that altitude is among the main factors determining carabid species distribution and community composition (e.g. Greenslade 1968; Holmes et al. 1993; Butterfield 1996). The altitudinal zonation of carabid fauna (Fig. 2) was similar to the altitudinal grouping of gnaphosid spiders in Crete and the total number of species (Chatzaki et al. 2005). Even though the latter have been proved to decline with altitude and follow a hump-shaped pattern, no significant altitudinal pattern of species richness was found for carabid richness in our study (Table 5).

The composition of carabid local assemblages did not differ among phryganic (CP, IP), and maquis (M) formations as well as the four grazing regimes recorded in our study (Table 2). Most of the Cretan carabids were widely distributed at all shrubland formations, except subalpine shrublands (SS), representing the typical carabid fauna of Crete (Trichas 1996). Besides, none exotic or idiosyncratic

species were identified in our study, all of them being native. However, the species-genus ratio of ground beetles per site on Crete was very low. Most genera were represented with very few species, which were generally homogenously distributed in the island. The low species-genus ratio of carabids was mainly due to the wide presence and dominance of strictly Cretan endemic taxa (Appendix 2) in all habitat types in the present study, contributing to a concept of an impoverished carabid fauna. Though the differentiation of carabid species composition among different habitat types (Jeanneret et al. 2003; Aviron et al. 2005) was statistically affirmed in our study (Table 3), this was due to the high dissimilarity of carabids at subalpine shrublands with all other habitat types. The altitudinal character of SS sites confirms the altitudinal pattern of carabid composition. Ground beetles in phryganic (CP, IP) and maquis sites (M) did not differ, because the Cretan endemic carabids were widely distributed and highly abundant at most study sites.

The 40 site assemblages were grouped into three broad carabid communities at low (C1, C2) and high altitudes (C3). Although, species composition per site was marginally similar among different grazing levels (Table 2), contrary to previous studies (McFerran et al. 1994; Dennis et al. 1997; Moran et al. 2012), *Platyderus jedlickai* proved to be a significant grazing indicator at G4 sites at low (C2) and high altitudes (C3) (Fig. 3). The dominant species in G5 sites, mainly *Carabus banoni*, showed a relatively lower abundance, compared to other sites. *C. banoni* and *Cymindis lineata* were significantly less abundant at G5 sites compared to sites with low grazing intensity (G2). Indeed, large *Carabus* species are known to exhibit very low abundances in areas under intensive grazing (Dennis et al. 1997; Cole et al. 2006), as well as other types of anthropogenic disturbance (e.g. Ribera et al. 2001; Elek and Lövei 2007).
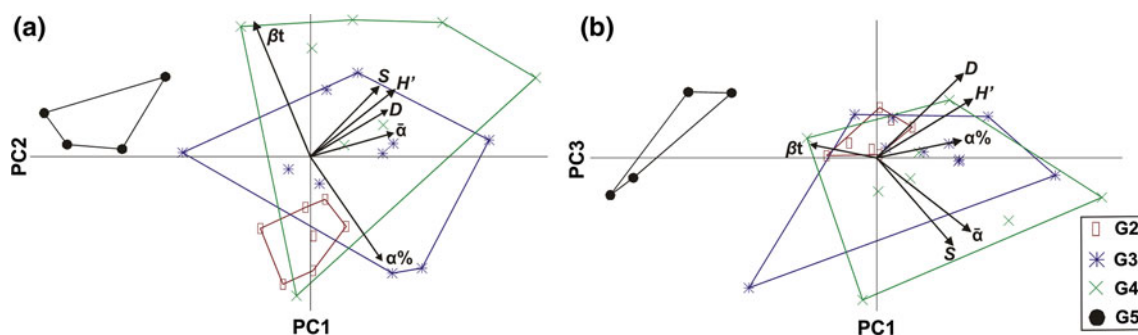
Fig. 5 PCA classification biplot of carabid site assemblages and the six measured variables (S, H′, D, ᾱ, α %, βt, as explained in Table 5). Value and importance of variables increase in the direction of the arrow. **a** PC1 versus PC2, **b** PC1 versus PC3. *Different symbols* indicate different levels of grazing (G2–G5)

Table 7 Percentage of significant paired-sites comparisons of the Shannon (H′) and Simpson (D) indices between classes of grazing intensity through permutation tests

	G2	G3	G4	G5
G2				
H′	28.57 %	77.14 %	73.21 %	57.14 %
D	28.57 %	82.86 %	66.07 %	64.29 %
G3				
H′		60.71 %	65.00 %	60.00 %
D		75.00 %	72.50 %	67.50 %
G4				
H′			84.44 %	71.87 %
D			86.67 %	71.87 %
G5				
H′				33.33 %
D				33.33 %

Diversity patterns

Regardless of which species were present, the general diversity and temporal dynamics of carabid site assemblages were determined by the level of grazing at the study sites (Table 5). Carabids at overgrazed sites (G5) comprised few species and generally sparse populations, as shown by the high percentage of singletons and the comparatively low species richness estimation (Table 1). Diversity was lowest and dominance was highest at G5 sites (Fig. 4b, c), as expected under severe disturbance (Connell 1978).

Our findings support the Intermediate Disturbance Hypothesis (IDH, Connell 1978): species richness, diversity and evenness were highest at G3 and G4 sites, following a hump-shaped pattern with grazing intensity (Table 5; Fig. 4a–c). According to theoretical predictions, competitive exclusion occurred at low disturbance levels, which resulted in low diversity, whereas richness and diversity increased at intermediate-high grazing levels, due

to successful competitive species, which occupied niche space, such as *Platyderus jedlickai*, a significant grazing indicator at G4 sites in communities C2 and C3 (Fig. 3). Wootton (1998) modeled the effects of disturbance on ecological communities and found that competitors at top trophic levels do not conform to the IDH, while basal species in food webs tend to follow the IDH. Considering the fact that Carabidae are high level consumers, our findings seem to contradict Wootton's results. Most of earlier studies focused on the response of ground beetles to urbanization (e.g. Niemelä et al. 2002; Elek and Lövei 2007) and supported the opportunistic species hypothesis (OSH) (Gray 1989), rather than IDH, confirming Wootton's (1998) results, as generalist species gained dominance in the most disturbed (urban) areas. However, the IDH has been previously confirmed for carabids in relation to grazing (Suominen et al. 2003). Apparently, the diversity patterns of carabids along disturbance regimes depend on the nature and intensity of perturbation, which may cause a significant change on the composition of local assemblages and/or reflect a differentiation of relative abundance distributions. The level of impact of different types of disturbance on natural communities is not the same and particularly regarding grazing, its impact on natural ecosystems as a disturbance has been widely debatable (Milchunas et al. 2008; Pykälä 2000). The level of disturbance caused by semi-domesticated goats and sheep on Crete is quite high, due to the absence of grazing control in various areas of the island and the apparent thinning or loss of natural shrub vegetation. Nevertheless, urbanization affects insect populations much more severely and directly through pollution and destruction of natural habitats (Pyle et al. 1981), leading to the direct mortality of indigenous arthropod species and their replacement by generalist species (McIntyre 2000; Elek and Lövei 2007). Though diversity was minimal at G5 sites in our study, mortality, which had the largest effect on the outcome of Wootton's (1998) models, was probably not high enough to cause a significant change of site assemblage composition in

relation to grazing (Table 2) as a consequence of species loss. This is mainly due to the common response of well adapted, dominant endemic species, such as *Carabus banoni* in our study.

The variation of diversity among different grazing classes was also detected on a temporal scale (Table 5). The alpha proportion as a quantitative measure of temporal turnover of beetle site assemblages (α %) was inversely proportional to temporal beta diversity (βt), in accordance with previous studies on aquatic macro-invertebrates (Romanuk and Kolasa 2001) and dung beetles (Zamora et al. 2007). Both measures were independent of species richness and were linearly related with increased grazing, negatively (α %) or positively (βt) (Fig. 4e, f).

The high variance of diversity among sites of G3 and G4 grazing classes (Table 7; Fig. 5) indicates that they represent broader ecological conditions, compared to the more strict patterns in G2 and G5 sites, which are determined by strong ecological restrictions, either competitive exclusion or resource limitation. Especially carabids at G5 sites shared very similar diversity patterns and temporal dynamics, which isolated them from the respective patterns at G2–G4 sites (Fig. 5). Temporal turnover was highest and temporal beta diversity was lowest at G2 sites, as a result of the longer phenologies of carabid species, contrary to local assemblages at G5 sites. Additionally, considering the generally low species richness at G2 sites, the assumption of domination by few highly tolerant species (Romanuk and Kolasa 2001) is confirmed. Fewer species were active during each sampling period at G5 sites and, regardless of the total species richness, their temporal co-occurrence was minimal compared to the other grazing classes, exhibiting an instability of temporal site assemblage organization.

Regarding the Mediterranean, the high temporal heterogeneity (high temporal β diversity) of dung beetles in W Mediterranean (Zamora et al. 2007) and darkling beetles in E Mediterranean (Kaltsas et al. 2012) was attributed to their good adaptation to the temporally changing ecological conditions in the region, in the form of drastic seasonality. However, the highest values of temporal species turnover in our study were exhibited by carabids at overgrazed or intensively grazed sites at central (KL, ZA) and southern Crete (LE, SL, AR), the west end (EL) and the east end (CH) of the island (Fig. 1), at different habitat types and altitudinal classes (Appendix 1). The ecological and geographical variation of the above-mentioned study sites rules out the interpretation of the high values of βt on drastic seasonality, taking into consideration the relatively small area of Crete and the finer scale in which our study was conducted. Since temporal beta diversity was independent of local species richness, the high βt values at overgrazed sites were a result of shifting phenologies of co-occurent species due to overgrazing and possible consequent habitat loss and resource

limitation. Such high temporal change of structure is attributed to degraded habitats due to strong perturbation (Romanuk and Kolasa 2001), and has been reported for carabids in overgrazed areas of the eastern Mediterranean, including Crete (Kaltsas et al. 2012).

Conservation relevance and conclusions

The present study highlights ground beetle assemblages as sensitive and well adapted to different grazing levels in shrublands of Crete. Carabids responded to grazing at the assemblage level, rather than species-specifically and their composition was mainly determined by altitude. Overgrazing and minimized resource availability led to low tolerance and consequently low abundance or absence of *Carabus banoni* and *Cymindis lineata*, which were the two most widely distributed species in Crete. Inversely, species that persist at overgrazed areas succeed in doing so by shifting their activity period, thus decreasing interspecific co-occurrence.

Grazing is an old-fashioned, traditional human activity and an essential part of historic ecosystems of Crete (Vogiatzakis and Rackham 2008). However, intensification and continuity of goat and sheep grazing during the last decades, have apparently led to habitat loss and increased dominance of nitrophilous bulb plants (e.g. *Asphodelus aestivus*, *Drimia maritima*) at several degraded shrub formations on the island. Estimation of grazing pressure and monitoring are difficult, because the reports on the specific numbers of livestock in Crete are unreliable and usually far from true (Rackham and Moody 1996). A seasonal change of grazing areas through an application and enforcement of management planning according to the priority of shrub biotopes for conservation (Dimopoulos et al. 2006) would enhance indigenous plant restoration and niche space of invertebrate fauna. Conservation prioritization should be given to diversity protection in terms of maintaining natural populations of indigenous and endemic species, especially those which are less tolerant to high disturbance levels. Although intense grazing (G4 in our study) favours the establishment of competitive species, such as Cretan endemic *Platyderus jedlickai*, a significant grazing indicator at G4 sites, few species are present at overgrazed sites (G5) in Crete. Further research is needed in order to prioritize conservation practice. Monitoring control surveys should focus on the co-occurrence patterns of species that colonize areas at intermediate/high grazing with species which are present at overgrazed sites. Potential competition patterns in relation to habitat loss and limited resource availability will highlight taxa of conservation importance.

Appendix 1

See Table 8.

Table 8 The sampling sites from east to west (1–40): their code names (as shown in Fig. 1), geographical coordinates (longitude, latitude), altitude (in m) and altitudinal zone, habitat type, level of grazing (G2–G5) and sampling period

	Site code	Longitude	Latitude	Altitude–alt. zone	Habitat type	Grazing level	Numer of traps	Sampling period
1	EL	23.541	35.272	30–ALT1	CP	G4	20	26/6/1996–7/71997
2	GP	23.594	35.573	400–ALT2	CP	G5	15	26/6/1996–12/7/1997
3	GK	23.606	35.558	140–ALT1	CP	G3	15	26/6/1996–12/7/1997
4	PH	24.465	35.166	250–ALT1	IP	G5	15	26/6/1996–12/7/1997
5	AM	24.663	35.176	760–ALT3	IP	G3	20	21/4/1999–15/4/2000
6	AC	24.7	35.242	720–ALT3	IP	G4	20	19/4/1999–15/4/2000
7	RI	24.731	35.127	250–ALT1	IP	G4	20	20/4/1999–16/4/2000
8	KL	24.741	35.193	650–ALT2	IP	G4	20	19/4/1999–14/4/2000
9	TI	24.747	35.287	1,090–ALT3	IP	G4	20	22/4/1999–7/4/2000
10	MA	24.755	34.938	160–ALT1	M	G3	20	23/12/1998–4/1/2000
11	KH	24.757	35.211	1,650–ALT4	SS	G3	15	2/7/2000–12/6/2001
12	AG	24.762	35.309	670–ALT2	IP	G3	20	22/4/1999–7/4/2000
13	KO	24.762	35.017	50–ALT1	CP	G5	20	2/2/1999–4/2/2000
14	GA	24.784	35.35	160–ALT1	IP	G2	20	22/4/1999–7/4/2000
15	LO	24.792	35.197	1,950–ALT4	SS	G3	15	2/7/2000–12/6/2001
16	PP	24.829	34.943	70–ALT1	CP	G4	20	2/2/1999–3/2/2000
17	PI	24.866	34.987	490–ALT2	IP	G3	20	2/2/1999–3/2/2000
18	MV	24.884	35.145	580–ALT2	IP	G3	20	16/4/1999–12/4/2000
19	ZA	24.911	35.142	490–ALT2	IP	G5	20	20/5/1999–2/7/2000
20	RF	24.931	35.163	1,100–ALT3	M	G4	20	16/4/1999–14/4/2000
21	DI	24.938	35.172	1,370–ALT3	M	G4	20	16/4/1999–14/4/2000
22	LE	24.941	34.937	70–ALT1	CP	G5	20	2/2/1999–3/2/2000
23	MI	24.946	34.993	340–ALT1	IP	G3	20	11/2/1999–3/2/2000
24	PA	24.992	35.077	280–ALT1	IP	G5	20	20/5/1999–2/7/2000
25	SL	25.086	34.989	600–ALT2	IP	G5	20	16/7/1996–21/7/1997
26	SH	25.086	34.985	720–ALT3	IP	G2	20	16/7/1996–21/7/1997
27	KS	25.09	34.959	750–ALT3	IP	G2	20	16/7/1996–21/7/1997
28	KD	25.092	34.951	520–ALT2	IP	G2	20	17/7/1996–25/7/1997
29	AR	25.229	34.983	750–ALT3	IP	G4	20	11/2/1999–26/1/2000
30	AN	25.339	35.014	210–ALT1	M	G4	20	26/1/1999–26/1/2000
31	KE	25.373	35	50–ALT1	CP	G5	20	26/1/1999–26/1/2000
32	OV	25.449	35.072	1,360–ALT3	IP	G4	20	26/1/1999–26/1/2000
33	LH	25.478	35.111	1,750–ALT4	SS	G2	15	8/5/2000–10/5/2001
34	LL	25.47	35.129	1,450–ALT3	SS	G3	15	8/5/2000–10/5/2001
35	SE	25.555	35.097	820–ALT3	IP	G4	20	5/1/1999–31/1/2000
36	PM	25.703	35.1	360–ALT1	IP	G2	20	5/1/1999–31/1/2000
37	KA	25.824	35.109	100–ALT1	M	G2	20	12/1/1999–1/2/2000
38	CG	25.833	35.087	140–ALT1	IP	G3	20	4/1/1999–1/2/2000
39	CH	26.205	35.037	150–ALT1	CP	G5	20	5/6/2000–5/6/2001
40	MT	26.221	35.233	170–ALT1	CP	G3	20	6/4/1997–24/3/1998

ALT1: 0–399 m, ALT2: 400–700 m, ALT3: 700–1,599 m, ALT4: 1,600–2,199 m. *CP* coastal phrygana, *IP* inland phrygana, *M* maquis, *SS* subalpine shrubland

Appendix 2

See Table 9.

Table 9 The total activity density (number of ind./100 trap-days) of the 42 captured carabid species at the 40 study sites

	AC	AG	AM	AN	AR	CG	CH	DI	EL	GA	GK	GP	KA
Calathus fuscipes Goeze, 1777	1.64	0.5	3.89	4.77	2.25	0	0	8.99	0	0	0	0	0
Cymindis lineata (Quensel, 1806)	0	0.04	19.6	0.26	0.2	0.61	0	36.2	0.42	0	0.11	2.08	0.73
Carabus banoni Dejean 1829[a]	4.79	6.59	5.96	2.77	4.56	7.38	6.88	10.9	1.21	6.69	17.3	6.32	5.92
Zabrus oertzeni Reitter, 1885[a]	0.23	0.76	2.59	0	0.35	0	0	2.65	0	0	0	0	0
Calathus oertzeni Jeanne & F. Battoni, 1988[a]	5.23	0	12.7	0	0	0.19	0	0	0.08	0	2.39	0.16	0
Tapinopterus creticus (I. Frivaldszky von Frivald, 1845)[a]	6.48	2.15	0	0	0	0	0	0	3.56	2.58	11.6	7.18	0.08
Acinopus picipes (Olivier, 1795)	0	0	0	0	0	0	0.56	0	0	0	0	0	0
Platyderus jedlickai Mařan, 1935[a]	0	0.47	0	0.75	0.8	0.62	0.07	0.46	0.14	0.76	0	0	3.3
Ophonus subquadratus (Dejean, 1829)	0.59	0	0	0.27	0	0.06	0	0	0.28	0	5.39	1.26	0
Harpalus honestus (Duftschmid, 1812)	0	0	0	0	0	0	0	0	0	0	0	0	0
Tapinopterus stepaneki Mařan, 1934[a]	0	0.9	0	0	0	0	0	0.13	0	0	0	0	0
Calosoma inquisitor (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditomus calydonius (P. Rossi, 1790)	0	0.35	0	0.44	0.2	0.73	0.1	0.83	0	2.23	3.01	0.08	0.32
Harpalus tenebrosus Dejean, 1829	0	0	0	0.18	0	0	0.3	0	0	0.51	0.21	0.08	0.11
Calathus mollis (Marsham, 1802)	0	0	0	0	0	0	0	0	0.81	0	0	0	0
Amara eurynota (Panzer, 1796)	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Ditomus obscurus (Dejean, 1825)	0	0	0	0	0	0	0	0	0	0	0.33	0	0
Dixus eremita (Dejean, 1825)	0.05	0.18	0.06	0	0.61	0	0	0	0	0	0	0	0.08
Zabrus graecus Dejean, 1828	0	0	0	0.51	0.3	0	0	0	0	0	0	0.39	0
Olisthopus glabricollis (Germar, 1817)	0.09	0	0	0.19	0.4	0	0	0.1	0	0	0	0	0
Licinus aegyptiacus Dejean, 1826	0	0	0	0	0	0	0	0	0	0	0.28	0.07	0
Carterus dama (P. Rossi, 1792)	0	0.07	0	0	0.19	0	0	0	0	0	0	0	0
Leistus spinibarbis (Fabricius, 1775)	0	0	0	0	0	0	0	0.09	0	0	0	0	0
Amara cretica Hieke, 2008	0	0	0	0	0	0	0	0	0	0	0	0	0
Trechus quadristriatus (Schrank, 1781)	0	0	0	0	0	0	0	0	0.1	0.2	0	0	0
Lebia cyanocephala (Linnaeus, 1758)	0	0	0.15	0	0	0	0	0	0	0	0	0	0
Nebria testacea Olivier, 1811	0	0	0	0	0.05	0	0	0	0	0	0	0	0
Amara aenea (DeGeer, 1774)	0	0	0	0	0	0	0	0	0	0	0	0	0
Cicindela campestris (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0
Notiophilus substriatus (Waterhouse, 1833)	0	0	0	0	0	0	0	0	0	0	0	0	0
Bembidion lampros (Herbst, 1784)	0	0	0	0	0	0	0	0	0	0	0	0	0
Microlestes maurus (Sturm, 1827)	0	0	0	0	0	0	0	0	0	0	0	0	0
Trechus austriacus Dejean, 1831[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Leistus fulvibarbis Dejean, 1826[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlaenius circumscriptus (Duftschmid, 1812)[b]	0	0	0	0.09	0	0	0	0	0	0	0	0	0
Calosoma sycophanta (Linnaeus, 1758)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlaenius festivus Panzer, 1796[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpalus rufipes (DeGeer, 1774)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Notiophilus geminatus (Dejean, 1831)[b]	0	0	0	0	0	0	0	0	0	0	0	0.08	0
Syntomus pallipes (Dejean, 1825)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpalus griseus (Panzer, 1796)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Syntomus obscuroguttatus (Duftschmid, 1812)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0

	KD	KE	KH	KL	KO	KS	LE	LH	LL	LO	MA	MI	MT
Calathus fuscipes Goeze, 1777	0	0	17.6	0.17	0	6.25	0.26	0	1.39	0.07	0	0.11	0
Cymindis lineata (Quensel, 1806)	6.11	0	76.5	1.49	0.09	2.67	0.09	7.97	6.45	0	0	0.24	6.32
Carabus banoni Dejean 1829[a]	16.2	0	4.47	2	3.8	13.3	5.2	10.3	3.31	1.06	13.6	8.69	10.6
Zabrus oertzeni Reitter, 1885[a]	0.17	0	9.92	0	0	0.75	0	0.63	16.8	2.44	0	0	0
Calathus oertzeni Jeanne & F. Battoni, 1988[a]	0	0	4.24	0	0	1.08	0	0	0	0	0.19	0.11	0

Table 9 continued

	KD	KE	KH	KL	KO	KS	LE	LH	LL	LO	MA	MI	MT
Tapinopterus creticus (I. Frivaldszky von Frivald, 1845)[a]	1.35	0	0	0	0	0.17	0	0	0	0.04	1.35	0.4	0
Acinopus picipes (Olivier, 1795)	0	0	20.6	0	0	0	0	0	0	15.8	0	0	0
Platyderus jedlickai Mařan, 1935[a]	0	1.26	0	0.37	0.3	0	0	0	0.26	0.92	2.43	0.22	0
Ophonus subquadratus (Dejean, 1829)	0	0.04	0	0	0.09	0	0.2	0	0	0	0	0.5	11.9
Harpalus honestus (Duftschmid, 1812)	0	0	5.58	0	0	0	0	2.01	0.35	11	0	0	0
Tapinopterus stepaneki Mařan, 1934[a]	0.18	0	2.59	0	0	0	0	0	0	0	0	0.21	0
Calosoma inquisitor (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	14.7	0	0	0
Ditomus calydonius (P. Rossi, 1790)	0.88	0	0	0.16	0.09	0	0	0	0	0	0.34	1.23	0
Harpalus tenebrosus Dejean, 1829	0.33	0	0	0	0.73	0	0.17	0	0	0	0.61	0.71	0.99
Calathus mollis (Marsham, 1802)	0	0	0	0.43	3.88	0	0	0	0	0	0	0	0.29
Amara eurynota (Panzer, 1796)	0	0	2.72	0	0	0	0	0.25	0	0.33	0	0	0
Ditomus obscurus (Dejean, 1825)	0	0	0.62	0	0	0.58	0	0	0	0	0	0	0
Dixus eremita (Dejean, 1825)	0	0.17	0	0	0	0	0	0	0	0	0	0	0
Zabrus graecus Dejean, 1828	0	0	0	0	0	0	0	0	0	0	0	0	0.25
Olisthopus glabricollis (Germar, 1817)	0	0	0	0.14	0	0	0	0	0	0	0	0	0
Licinus aegyptiacus Dejean, 1826	0	0	0	0	0	0	0.26	0	0	0	0	0.09	0.29
Carterus dama (P. Rossi, 1792)	0	0.08	0	0	0	0	0	0	0	0	0	0	0
Leistus spinibarbis (Fabricius, 1775)	0	0	0	0	0	0	0	0	0	0	0	0	0
Amara cretica Hieke, 2008	0	0	0	0	0	0	0	0	0	0	0	0	0.82
Trechus quadristriatus (Schrank, 1781)	0	0	0	0	0	0	0	0	0	0	0	0	0
Lebia cyanocephala (Linnaeus, 1758)	0	0	0.53	0	0	0	0	0	0	0	0	0	0
Nebria testacea Olivier, 1811	0	0	0.26	0	0	0	0	0	0	0	0	0	0
Amara aenea (DeGeer, 1774)	0	0	0	0	0	0	0	0	0.25	0	0	0	0
Cicindela campestris (Linnaeus, 1758)	0	0	0.44	0	0	0	0	0	0	0	0	0	0
Notiophilus substriatus (Waterhouse, 1833)	0	0	0	0	0	0	0	0	0	0	0	0	0
Bembidion lampros (Herbst, 1784)	0	0	0	0	0	0	0	0	0	0	0	0	0
Microlestes maurus (Sturm, 1827)	0	0	0	0	0	0	0	0	0	0	0	0	0
Trechus austriacus Dejean, 1831[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Leistus fulvibarbis Dejean, 1826[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlaenius circumscriptus (Duftschmid, 1812)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Calosoma sycophanta (Linnaeus, 1758)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlaenius festivus Panzer, 1796[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpalus rufipes (DeGeer, 1774)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Notiophilus geminatus (Dejean, 1831)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Syntomus pallipes (Dejean, 1825)[b]	0	0	0	0	0	0	0	0	0.08	0	0	0	0
Harpalus griseus (Panzer, 1796)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0
Syntomus obscuroguttatus (Duftschmid, 1812)[b]	0	0	0	0.05	0	0	0	0	0	0	0	0	0

	MV	OV	PA	PH	PI	PM	PP	RF	RI	SE	SH	SL	TI	ZA
Calathus fuscipes Goeze, 1777	0.27	587	2.81	0	0	0	0	2.39	0.16	13.4	13.3	0.24	31.2	0
Cymindis lineata (Quensel, 1806)	0.08	103	0	0	1.22	0.5	0	0.08	0	2.1	1.73	0	0	0
Carabus banoni Dejean 1829[a]	2.81	10.5	2.52	2.67	21.8	11	1.58	4.17	4.01	1.45	2.32	1.85	20.2	1.89
Zabrus oertzeni Reitter, 1885[a]	0	14.5	0	0	0	0	0.1	7.17	0	0	24.4	0.15	5.92	0
Calathus oertzeni Jeanne & F. Battoni, 1988[a]	0	0.18	0	0	0	0	0	47.4	0.08	1.11	0	0	10.1	0
Tapinopterus creticus (I. Frivaldszky von Frivald, 1845)[a]	3.16	0.09	0.21	2.93	0.14	4	0	0.42	0	0	0	0	14.6	0
Acinopus picipes (Olivier, 1795)	0	0	0	0	0	0	0	0	0	0	0	0	0.42	0
Platyderus jedlickai Mařan, 1935[a]	0.31	1.11	0	0	0.08	1.3	0.89	5.04	0	0.18	0	0	1.89	0
Ophonus subquadratus (Dejean, 1829)	0.04	0	0	0.83	0	0	0.17	0	0.78	0	0	0	0	0.13
Harpalus honestus (Duftschmid, 1812)	0	0.18	0	0	0	0	0	0	0	0	0	0	0.19	0
Tapinopterus stepaneki Mařan, 1934[a]	0	0.09	0	0	0.35	0	0	0.53	0	0	0	0	14.2	0
Calosoma inquisitor (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ditomus calydonius (P. Rossi, 1790)	0.27	0	0.08	0.22	1.01	0	0	0.09	0.28	0.27	0	0	0	1.03
Harpalus tenebrosus Dejean, 1829	0	0	0	0	0	0.2	0.47	0	0	0.64	0.08	0	0	0
Calathus mollis (Marsham, 1802)	0	0	0	0	0	0	0	0	0	0	0.24	0	0.19	0
Amara eurynota (Panzer, 1796)	0.04	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 9 continued

	MV	OV	PA	PH	PI	PM	PP	RF	RI	SE	SH	SL	TI	ZA
Ditomus obscurus (Dejean, 1825)	0	0	0	0	0	0	0	0	0	0	0.71	1.02	0	0
Dixus eremita (Dejean, 1825)	0	0.7	0	0.11	0	0	0	0	0	0.1	0	0	0	0
Zabrus graecus Dejean, 1828	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Olisthopus glabricollis (Germar, 1817)	0.16	0	0	0	0	0	0	0	0	0.18	0	0	0.12	0
Licinus aegyptiacus Dejean, 1826	0.09	0	0	0	0.24	0	0	0	0	0	0	0	0	0
Carterus dama (P. Rossi, 1792)	0	0	0.08	0	0.56	0	0	0	0	0	0	0	0	0
Leistus spinibarbis (Fabricius, 1775)	0	0	0	0	0.09	0	0	0.28	0	0.43	0	0	0	0
Amara cretica Hieke, 2008	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trechus quadristriatus (Schrank, 1781)	0	0	0	0.1	0	0	0.09	0.11	0	0.07	0	0	0.12	0
Lebia cyanocephala (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0.08	0	0	0
Nebria testacea Olivier, 1811	0	0	0.05	0	0	0	0	0.11	0	0.09	0	0	0.04	0
Amara aenea (DeGeer, 1774)	0	0	0	0	0	0	0	0.09	0	0	0	0	0.19	0
Cicindela campestris (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notiophilus substriatus (Waterhouse, 1833)	0	0	0	0	0	0	0	0.11	0	0.07	0	0.17	0	0
Bembidion lampros (Herbst, 1784)	0	0	0	0	0	0	0	0	0	0.27	0	0	0	0
Microlestes maurus (Sturm, 1827)	0	0	0	0.11	0	0	0	0.11	0	0	0	0	0	0
Trechus austriacus Dejean, 1831[b]	0	0	0	0	0	0	0	0.11	0	0	0	0	0	0
Leistus fulvibarbis Dejean, 1826[b]	0	0	0	0	0	0	0	0	0	0.09	0	0	0	0
Chlaenius circumscriptus (Duftschmid, 1812)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calosoma sycophanta (Linnaeus, 1758)[b]	0	0.09	0	0	0	0	0	0	0	0	0	0	0	0
Chlaenius festivus Panzer, 1796[b]	0	0.09	0	0	0	0	0	0	0	0	0	0	0	0
Harpalus rufipes (DeGeer, 1774)[b]	0	0	0.08	0	0	0	0	0	0	0	0	0	0	0
Notiophilus geminatus (Dejean, 1831)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Syntomus pallipes (Dejean, 1825)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpalus griseus (Panzer, 1796)[b]	0.08	0	0	0	0	0	0	0	0	0	0	0	0	0
Syntomus obscuroguttatus (Duftschmid, 1812)[b]	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species are sorted from the most to the least abundant. [a] Cretan endemic species, [b] singletons

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