

## Co-occurrence patterns and shaping processes of assembly in beetle and spider communities in eastern Mediterranean maquis formations

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The patterns of assembly in ground beetle and ground spider communities were studied over two years in five juniper-maquis formations in the eastern Mediterranean (Greece and Cyprus). Comparative measures of plant cover, density and soil pH values revealed an earlier successional stage in two of the study sites (Crete, Cyprus), due to goat overgrazing, compared to the biotopes in Attiki, Naxos and Samos. Disturbance partially affected the total abundance, co-occurrence and niche overlap patterns within beetle communities. Spider communities were not affected by differential grazing intensity, with the exception of the right-skewed body size-frequency distributions (dominance of smaller species) in Crete and Cyprus. The community of carabids in Attiki showed significantly segregated co-occurrence patterns, due to microhabitat differentiation and shifting in phenology among competing sympatric *Carabus* species. Our study supports the annual inconsistency of co-occurrence patterns in insular areas and the generality of the decreasing body size (smaller species) hypothesis in increased disturbance levels in the eastern Mediterranean region.

**Key words:** Carabidae, Gnaphosidae, Greece, Cyprus, body size distribution.

### INTRODUCTION

One of the most interesting and strong debates in community ecology for almost a century is based on the dilemma of an organized system *versus* a haphazard co-occurrence of populations which form communities in nature (Krebs, 1985). According to many scientists, all communities have detectable limits and unique organization patterns, which are determined by “assembly rules” (Diamond, 1975), due to deterministic mechanisms such as competition (e.g. Gotelli & Ellison, 2002; Sanders *et al.*, 2003). The opposing school of ecologists considers communities as stocha-

stic assemblies of species, which independently adapt to local environmental conditions (Connor & Simberloff, 1979). The study of co-occurrence patterns, which reflects species interactions within communities, is a major field of community ecology (Gotelli & Ellison, 2002).

According to the theoretical predictions of Diamond’s assembly rules (Diamond, 1975), in the case of interspecific competition, species co-occur less than expected by chance. The affirmation of assembly rules is usually tested with null models (Gotelli & Graves, 1996). In addition, co-occurring species are expected to differ significantly in body size (Hutchinson, 1959), in order to minimize overlap in resource utilization (MacArthur & Levins, 1967; Schoener, 1974). Species body size distributions are a useful

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tool for understanding the shaping of species assembly and energy use within communities (Gotelli & Graves, 1996). Gotelli & Ellison (2002) were the first who tested the body size overlap of co-occurring ant species in New England. Nevertheless, the results of all community analyses depend on the spatial scale of study (Levin, 1992), and disturbance history (Sanders *et al.*, 2003), although the influence of disturbance on species co-occurrence patterns is poorly studied (Ulrich *et al.*, 2010).

The potential presence and prevalence of competition in animal communities has been the subject of a strong debate (Strong *et al.*, 1984). Ground beetle communities are among the most extensively studied arthropod communities and, although interspecific competition and resource partitioning have been reported in several studies on carabids, the presence of competition in carabid communities is doubted (Loreau, 1990, 1992; Niemelä, 1993). However, segregational patterns have arisen in recent studies on ground beetles (Ulrich & Zalewski, 2006) as well as arachnid taxa, such as spiders (Ulrich *et al.*, 2010), implying variant co-occurrence patterns in relation to anthropogenic disturbance. Besides, small carabid species are reported to dominate in highly disturbed habitats, contrary to less disturbed areas (e.g. Blake *et al.*, 1994).

The aim of our study was to explore the co-occurrence patterns and unveil possible effects of competition in communities of carnivorous beetle (Coleoptera: Carabidae) and spider (Araneae: Gnaphosidae)

epigeal families, which are dominant in terms of abundance in the eastern Mediterranean region (Trichas, 1996; Chatzaki, 2003). To test whether these patterns differed in relation to disturbance, we conducted our study in five eastern Mediterranean mosaic-like maquis formations with two levels of grazing intensity (two overgrazed sites – three relatively undisturbed areas).

## MATERIALS AND METHODS

### Study sites

The study was carried out in five similar areas in terms of their dominant woody plant species, *Juniperus phoenicea* and *Pistacia lentiscus*. The localities of the sites are: a) Pacheia Ammos in NE Crete (35° 6'35''N, 25° 49'9''E), b) Moutsouna in E Naxos (37° 2'46''N, 25° 34'27''E), c) Agia Marina in NE Attiki (38° 10'57''N, 24° 3'12''E), d) Psili Ammos in SE Samos (37° 42'26''N, 27° 1'29''E), and e) Kourio in S Cyprus (34° 40'3''N, 32° 51'48''E) (Fig. 1). The geological formation is limestone and the average altitude is approximately 40 m at all sites. Mean monthly values of abiotic factors (air temperature, air relative humidity and precipitation) at the study sites were strongly correlated (Pearson's  $r > 0.8$ ,  $n = 24$ ,  $p < 0.001$  at all paired comparisons). Generally, the climate was typical Mediterranean with high mean monthly air temperature (20 °C) and low annual precipitation (445 mm × year<sup>-1</sup>), 65% of which occurred during the cold months (November-February).

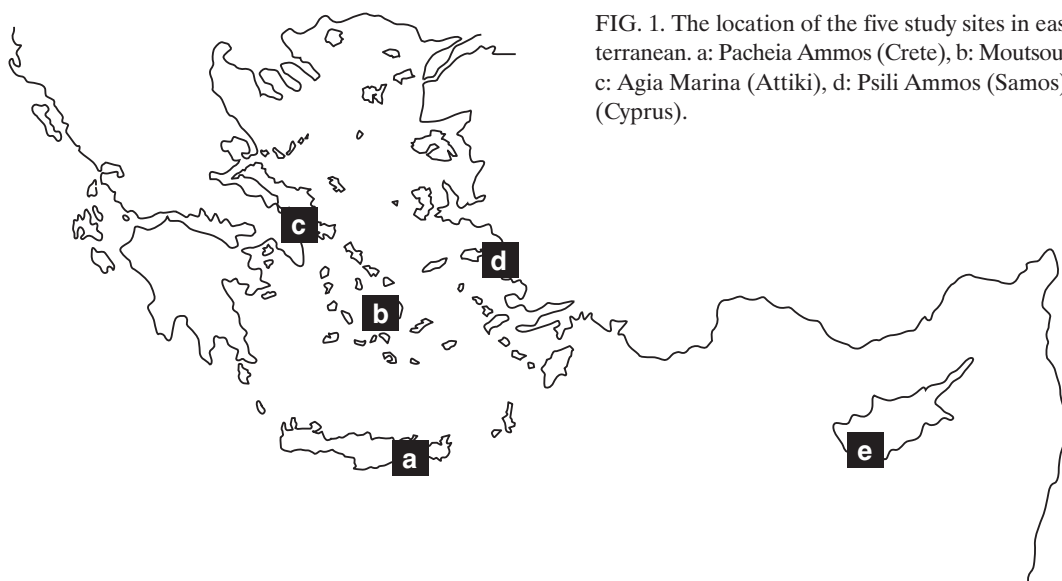


FIG. 1. The location of the five study sites in eastern Mediterranean. a: Pacheia Ammos (Crete), b: Moutsouna (Naxos), c: Agia Marina (Attiki), d: Psili Ammos (Samos), e: Kourio (Cyprus).

### Successional stage

The successional stage in the five sampling sites was determined through: a) the cover and density of the two dominant maquis species, *Juniperus phoenicea* and *Pistacia lentiscus* in relation to the cover and density of *Sarcopoterium spinosum*, a highly competitive phryganeic species, which replaces maquis species under intensive grazing in the E Mediterranean (Tzanopoulos et al., 2007), and b) the comparison of soil pH values. During successional stages, the abundance of *J. phoenicea* increases at relatively low pH values (Tzanopoulos et al., 2007). Soil pH was measured by pH meter in a 1:1 mixture of soil and distilled water. Ten soil samples per site were collected during the litter-fall period of *J. phoenicea* (March-May, May-July). Analysis was made using Kruskal-Wallis test and post-hoc comparisons using multiple comparisons test in STATISTICA 6.0 (StatSoft Inc., 2001).

### Sampling design

The study was conducted from May 2006 to May 2008 using pitfall traps (plastic containers 12 cm tall, 9.5 cm diameter at the top), containing propylene glycol as preservative and placed flush with the ground surface. The traps were set at the centre of the maquis formations and were changed at two months intervals. In order to cover a broad area within each study site, we placed three transects of traps at all sites, each including seven traps with 10 m inter-trap distance. The distance between two transects was 60–200 m. The 21 traps covered the three major microhabitat types of the study areas equally; dense vegetation and litter cover (*ps*), scarce vegetation (*p*) and open areas (*o*) (seven traps per microhabitat type).

### Taxonomic identification

Adult Carabidae and Gnaphosidae, the most abundant carnivorous arthropod families in our study, were identified to species and subspecies level, where possible. Nomenclature follows respectively Löbl & Smetana (2003) and Platnick (2010), including taxonomic additions/changes thereafter. The material is deposited in the Coleoptera and Araneae collections of the Natural History Museum of Crete, and a small part is deposited in the Coleoptera collection of the National Museum of Natural History, in Sofia, Bulgaria.

### Data analysis

#### Species richness

Species richness for each community was estimated using three nonparametric incidence-based estimators that calculate species-by-sample data: bootstrap, ICE and Jackknife1 (detailed description in Colwell, 2009). Accumulation curves were produced to examine if the local inventories could be considered as an adequate description of their richness, using the EstimateS 8.2.0 software package based on the mean of 50 randomizations (Colwell, 2009), taking into account the number of individuals as a surrogate for the sampling effort. In case of low sampling efficiency, the respective communities were excluded from further analyses.

#### Species co-occurrence

We used null model analyses (Gotelli & Graves, 1996) to examine species co-occurrence patterns. Presence-absence matrices were constructed for each community, with species as rows, and pitfall traps as columns ( $n = 21$ ). The observed C-score index was compared to values generated in 3000 simulations in Ecosim 7.72 (Gotelli & Entsminger, 2010), using a fixed-fixed model, where the row and column sums of the original matrix were maintained. Null matrices were generated using the sequential swap randomization algorithm and results for different communities were compared using the Standardized Effect Size (SES) (Gotelli & Entsminger, 2010). Although there is no evidence of competition between carabids and gnaphosids, we also analyzed matrices including both beetle and spider taxa.

In case of a significant C-score, we identified the species which contributed mostly to the non-random co-occurrence patterns, participating in pairs with observed number of Checkerboard Units (CU) in the 95<sup>th</sup> percentile of all pairwise combinations. Non-random associations between species were assessed using the Pairs program with 100 randomizations (Ulrich, 2008). Possible competitive interactions between these species were traced through their niche overlap and comparative phenological patterns. Probability level error rates were corrected according to the method of Benjamini & Yekutieli (2001), which does not assume the tests (iterations) to be independent, contrary to the Bonferroni method (Gotelli & Ulrich, 2010).

### Body size overlap and distribution

Body size data were ranked and  $\log_{10}$ -transformed, and the difference between adjacent (in size) species was calculated. The variance in these “segment lengths” ( $\sigma^2$ ) is larger in cases of higher heterogeneity in size ratios of adjacent species (Gotelli & Ellison, 2002). Hence, in a competitively structured community, the observed variance should be significantly less than expected by chance (Gotelli & Entsminger, 2010). We used the uniform null model application, in which the endpoints of the distribution are fixed by the largest and smallest species in each assemblage (EcoSim 7.72 with 1000 iterations – Gotelli & Entsminger, 2010). Since the five areas differ in isolation and suitability for colonization and the captured species belong to different biogeographic source pools, we analyzed the five sites separately, rather than as “replicates” within an archipelago (Gotelli & Graves, 1996).

The shape of the body size-frequency distribution was assessed through measures of skewness (Ulrich *et al.*, 2008). Negative values (left-skewed distribution) correspond to dominance of larger species, whereas positive skewness (right-skewed distribution) is related to prevalence of smaller species.

Body size of beetles was quantified as the body length of each species (Jarošik, 1989). Carapace width was chosen as our size trait of spider body size (Hagstrum, 1971). Body length for each species was measured as the average of the lengths of five male and five female individuals, an adequate number for arthropod taxa (Gotelli & Ellison, 2002). Intraspecific length variation of spiders between sites was included, due to the fact that the body size of spiders is possible to vary significantly among adults. In order to test for possible competition patterns, we exclusively included species with similar feeding habits in null model analyses. Therefore, herbivore ground beetles (*Acinopus picipes*, *Ditomis calydonius*, *Dixus eremita*, *Ophonus subquadratus*, and an uncertain species of *Zabrus*) (see online supplementary material, Table S1) were excluded from all co-occurrence and body size analyses.

### Phenological patterns

The phenological patterns of beetles and spiders were analyzed using circular statistics in Oriana 2.02 software (Kovach, 2004). Sampling time intervals were converted to angles (intervals of  $60^\circ$ ) and total bi-monthly activity density was included in the analyses

as the frequency of angle interval. Rayleigh Uniformity test was used to calculate the probability that the data are uniformly distributed around the analyzed cycle. A significant result indicates a significant mean angle (Kovach, 2004), i.e. a statistically significant phenological pattern. The phenologies of communities/species were compared using the Watson-William F-test. The distribution of phenological data was found through their fitting to the von Mises distribution using the Kuiper’s Test (Kovach, 2004). The von Mises distribution is a unimodal distribution which is the circular analogue of the normal distribution in linear data (Evans *et al.*, 2000).

### Microhabitat preference and niche overlap

To determine whether different microhabitat types differed in their abundance of species, we applied Analysis of Similarities (ANOSIM) with 999 permutations (Clarke, 1993) in PRIMER v5.0 software. Common and rare species were equally weighted with square root transformation of data. SIMPER analysis (Clarke, 1993) was used to determine the contribution of each species to the average Bray-Curtis dissimilarity between microhabitats.

We applied null models to generate null distributions of assemblage-wide niche overlap. As a measure of niche, we implemented microhabitat type and temporal activity time, two of the three most important niche axes according to Schoener (1974). We used the relative abundance of each species in every microhabitat type and sampling period ( $3 \times 6$  matrices), and applied random algorithm 2 (RA2), to retain the zero structure of the data which represents utilization constraints, with 1000 iterations in EcoSim 7.72 (Gotelli & Entsminger, 2010).

## RESULTS

### *Successional stage*

The cover and density of *S. spinosum* in Cyprus and (especially in) Crete were approximately three times higher than in Attiki, Naxos and Samos. On the contrary, *J. phoenicea* and *P. lentiscus* density was, respectively, 1.5 and 2 times lower in Cyprus and Crete compared to the rest three sites. Kruskal-Wallis ANOVA showed that soil pH values differed between the study sites (March-May:  $H = 33.937$ ,  $p < 0.001$ ; May-July:  $H = 34.193$ ,  $p < 0.001$ ) and the multiple comparisons test showed that this was due to the higher soil pH values in Cyprus and in Crete, compared to the

other three sites ( $p < 0.05$  in all cases), which is indicative of an earlier successional stage in Crete and Cyprus due to overgrazing.

*Composition of communities*

In total, we collected 32 carabid species (1151 individuals) (see online supplementary material, Table S1) and 38 gnaphosid species (1057 individuals) (see online supplementary material, Table S2). Species of the genus *Carabus* were the most abundant in the sites where dominance was evident in ground beetle communities (Attiki, Naxos, Samos). *Pterotricha lentiginosa* and species of *Zelotes* (*Z. tenuis* in Naxos, *Z. solstitialis* in Cyprus) were the dominant gnaphosid taxa, except Attiki, where *Berinda ensigera* exhibited the highest relative abundance. On Crete *P. lentiginosa* and *Trachyzelotes malkini* were co-dominant.

*Species richness*

Based on the average of the three richness estimators, pitfall sampling was efficient for all communities, except carabids in Cyprus, and gnaphosids in Attiki (Table 1), the communities with the lowest total number of captures (see online supplementary material, Tables S1 and S2). This was also evident in the curvature of the respective accumulation curves, which were far from reaching an asymptotic phase (Fig. 2). Therefore, both aforementioned communities were excluded from null model analyses.

*Species co-occurrence*

Generally, observed C-scores did not differ significantly from expected C-scores generated by null models (Table 2), indicating a random structure of most studied communities. The exception to random as-

TABLE 1. Species richness estimators for each study site. *S*: number of species collected at each site. Percentage represents the proportion of the number of species expected:  $(S/\text{mean estimation}) \times 100$ . Low sampling completeness is highlighted with bold characters

|             | Study site | <i>S</i> | ICE   | Jackknife1 | Bootstrap | Mean estimation $\pm$ SD | Sampling completeness % |
|-------------|------------|----------|-------|------------|-----------|--------------------------|-------------------------|
| Carabidae   | Crete      | 6        | 6.59  | 6.92       | 6.61      | 6.71 $\pm$ 0.19          | 89.46                   |
|             | Attiki     | 7        | 7.59  | 7.92       | 7.58      | 7.70 $\pm$ 0.19          | 90.95                   |
|             | Naxos      | 10       | 11.06 | 11.83      | 10.93     | 11.45 $\pm$ 0.54         | 87.37                   |
|             | Cyprus     | 11       | 26.37 | 17.42      | 13.61     | 21.9 $\pm$ 6.33          | <b>50.24</b>            |
|             | Samos      | 12       | 12.68 | 12.92      | 13.03     | 12.8 $\pm$ 0.17          | 93.75                   |
| Gnaphosidae | Crete      | 14       | 14.46 | 14.92      | 15.02     | 14.80 $\pm$ 0.3          | 94.59                   |
|             | Attiki     | 12       | 17    | 16.58      | 14.27     | 15.95 $\pm$ 1.47         | <b>75.24</b>            |
|             | Naxos      | 10       | 10.42 | 10.92      | 10.71     | 10.68 $\pm$ 0.25         | 93.60                   |
|             | Cyprus     | 11       | 11.31 | 11.92      | 11.55     | 11.59 $\pm$ 0.31         | 94.88                   |
|             | Samos      | 15       | 15    | 15         | 16.14     | 15.38 $\pm$ 0.66         | 97.53                   |

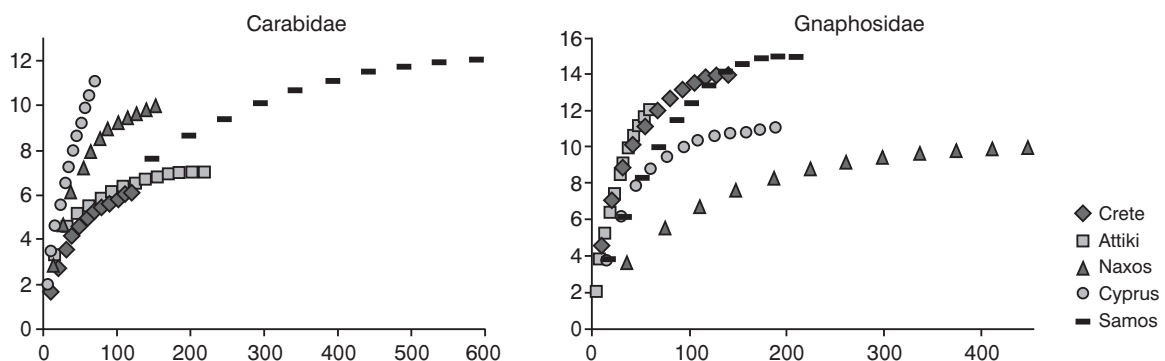


FIG. 2. Individual-based accumulation curves for the studied communities.



TABLE 2. Null model results of co-occurrence patterns in the beetle and spider communities. Observed C-scores (Obs. C-score) are compared to the average of 3000 simulated C-scores (Av. Sim. C-score). The variance of simulated C-scores is also included. Significant results ( $p$ -value and SES) are highlighted with bold characters

| Total     | CARABIDAE    |                  |                   |                 |             | GNAPHOSIDAE  |                  |                   |      |       |
|-----------|--------------|------------------|-------------------|-----------------|-------------|--------------|------------------|-------------------|------|-------|
|           | Obs. C-score | Av. Sim. C-score | Var. Sim. C-score | $p$             | SES         | Obs. C-score | Av. Sim. C-score | Var. Sim. C-score | $p$  | SES   |
| Crete     | 4.67         | 4.26             | 0.39              | 0.4             | 0.66        | 4.93         | 4.97             | 0.02              | 0.45 | -0.26 |
| Attiki    | 9.38         | 7.46             | 0.1               | <b>&lt;0.01</b> | <b>5.46</b> | —            | —                | —                 | —    | —     |
| Naxos     | 4.93         | 4.99             | 0.04              | 0.47            | -0.31       | 3.06         | 3.25             | 0.02              | 0.03 | -1.55 |
| Cyprus    | —            | —                | —                 | —               | —           | 5.11         | 4.99             | 0.02              | 0.21 | 0.8   |
| Samos     | 2.07         | 1.96             | 0.05              | 0.31            | 0.47        | 1.92         | 2                | 0.03              | 0.35 | -0.5  |
| 2006-2007 | Obs. C-score | Av. Sim. C-score | Var. Sim. C-score | $p$             | SES         | Obs. C-score | Av. Sim. C-score | Var. Sim. C-score | $p$  | SES   |
| Crete     | 3.67         | 3.92             | 0.7               | 0.92            | -0.3        | 9.55         | 9.67             | 0.04              | 0.3  | -0.63 |
| Attiki    | 12.81        | 10.15            | 0.24              | <b>&lt;0.01</b> | <b>5.37</b> | —            | —                | —                 | —    | —     |
| Naxos     | 5.2          | 4.84             | 0.16              | 0.21            | 0.89        | 3.22         | 3.28             | 0.06              | 0.49 | -0.24 |
| Cyprus    | —            | —                | —                 | —               | —           | 12.41        | 12.07            | 0.06              | 0.1  | 1.4   |
| Samos     | 11.1         | 11               | 0.25              | 0.36            | 0.25        | 2.98         | 3.03             | 0.05              | 0.48 | -0.19 |
| 2007-2008 | Obs. C-score | Av. Sim. C-score | Var. Sim. C-score | $p$             | SES         | Obs. C-score | Av. Sim. C-score | Var. Sim. C-score | $p$  | SES   |
| Crete     | 6.33         | 5.85             | 0.25              | 0.51            | 0.97        | 4.87         | 4.84             | 0.02              | 0.4  | 0.25  |
| Attiki    | 12.1         | 8.99             | 0.19              | <b>&lt;0.01</b> | <b>7.06</b> | —            | —                | —                 | —    | —     |
| Naxos     | 8.8          | 8.97             | 0.07              | 0.33            | -0.64       | 12.44        | 11.89            | 0.17              | 0.09 | 1.35  |
| Cyprus    | —            | —                | —                 | —               | —           | 8.82         | 8.67             | 0.1               | 0.28 | 0.47  |
| Samos     | 6.76         | 6.33             | 0.25              | 0.2             | 0.86        | 4.92         | 5.17             | 0.09              | 0.23 | -0.84 |

sembly was the community of carabids in Attiki, for which the observed C-score was significantly higher than expected by chance (in total and separately for each of the two years of study), revealing species segregation. The result for gnaphosids in Naxos was close to a significant aggregation ( $p = 0.03$ ). The tendency to aggregation was affirmed for the first year of study, though a segregated pattern was close to significance for the second year. This was the community with the most converse co-occurrence patterns in the two consecutive years of study, one of which close to significance. Consistency of co-occurrence was ev-

ident for all communities in Attiki and Samos. Analyses of mixed (beetle and spider) matrices showed that the co-occurrence patterns among the two studied groups were random at all sites ( $-0.75 < \text{SES} < 0.317$ ,  $0.223 < p < 0.479$ ).

Non-random associations of species-pairs were only detected for the community of carabids in Attiki (Table 3). Specifically, *Carabus hortensis* was significantly segregated with its congeners *C. graecus* and *C. coriaceus*, and the pairs formed by these three species were those with the highest observed number of CU. The co-occurrence pattern of gnaphosid spiders

TABLE 3. Significant co-occurrence of pairs of carabid species in Attiki. Significant standardized (Z transformed) effect sizes and the lower and upper Bayes confidence limit (CL) criterion are included. Significant  $p$ -values after the Benjamini & Yekutieli (2001) correction are highlighted with bold lettering

| Pairs   | Sig. Z-score | Lower CL | Upper CL | $p$                                  |
|---|--------------|----------|----------|--------------------------------------|
| <i>Carabus hortensis</i> – <i>Carabus graecus</i>   | 4.33         | 0.06     | 0.39     | <b><math>10^{-5}</math></b>          |
| <i>Carabus hortensis</i> – <i>Carabus coriaceus</i> | 4.28         | 0.06     | 0.56     | <b><math>2 \times 10^{-5}</math></b> |
| <i>Carabus graecus</i> – <i>Carabus coriaceus</i>   | 2.07         | 0.06     | 0.39     | 0.04                                 |

TABLE 4. Null model analyses results of beetle and spider body size overlap and skewness of body size-frequency distributions. In each community, the observed index (Obs. index) is compared to the average of 1000 simulated communities (Av. Sim. index). The variance of the simulated index was  $<0.001$  for all analyses

|             |        | Obs. index           | Av. Sim. index | <i>p</i> | SES    | Skewness |
|-------------|--------|----------------------|----------------|----------|--------|----------|
| Carabidae   | Crete  | 0.008                | 0.041          | 0.114    | -1.062 | 0.847    |
|             | Attiki | 0.002                | 0.009          | 0.028    | -1.234 | -2.042   |
|             | Naxos  | 0.018                | 0.024          | 0.401    | -0.442 | -1.773   |
|             | Cyprus | —                    | —              | —        | —      | 0.934    |
|             | Samos  | 0.015                | 0.021          | 0.39     | -0.465 | -2.707   |
| Gnaphosidae | Crete  | $6.8 \times 10^{-4}$ | 0.001          | 0.225    | -0.751 | 0.505    |
|             | Attiki | —                    | —              | —        | —      | -0.564   |
|             | Naxos  | $7.1 \times 10^{-4}$ | 0.001          | 0.179    | -0.840 | 0.001    |
|             | Cyprus | $4.3 \times 10^{-4}$ | 0.001          | 0.079    | -1.060 | 0.640    |
|             | Samos  | $8.7 \times 10^{-4}$ | 0.002          | 0.203    | -0.799 | -1.608   |

in Naxos was due to the maximal co-occurrence of the two most abundant species, *P. lentiginosa* and *Z. tenuis* (no participation in CU), during the first year of study. On the contrary, the tendency to significant segregation during the second year was mainly due to mutual avoidance between the congeneric *Zelotes solstitialis* and *Z. subterraneus* (maximal number of CU). Observed co-occurrence between *P. lentiginosa* and *Z. tenuis* was 100% during 2006-2007 and 85.7% during 2007-2008, whereas between *Z. solstitialis* and *Z. subterraneus* it was 42.9% during the first year and only 19% during the second year.

#### Body size overlap and distribution

The body size distributions of beetles and spiders on the study sites were generally not significantly different

from what would be expected by chance (Table 4). Non-random variance in segment length, i.e. non-overlapping body sizes among species, was not found for any beetle/spider community after the Benjamini & Yekutieli (2001) correction. The only analysis close to significance was for carabids in Attiki ( $p = 0.028$ ). The skewness of body size-frequency distribution of all communities in highly disturbed sites (Crete, Cyprus) was positive, contrary to all other beetle and spider communities in Attiki, Naxos and Samos, except gnaphosids in Naxos (normal distribution) (Table 4).

#### Phenological patterns

Rayleigh Uniformity test showed that the phenological patterns of all beetle and spider communities were statistically significant, except for carabids in

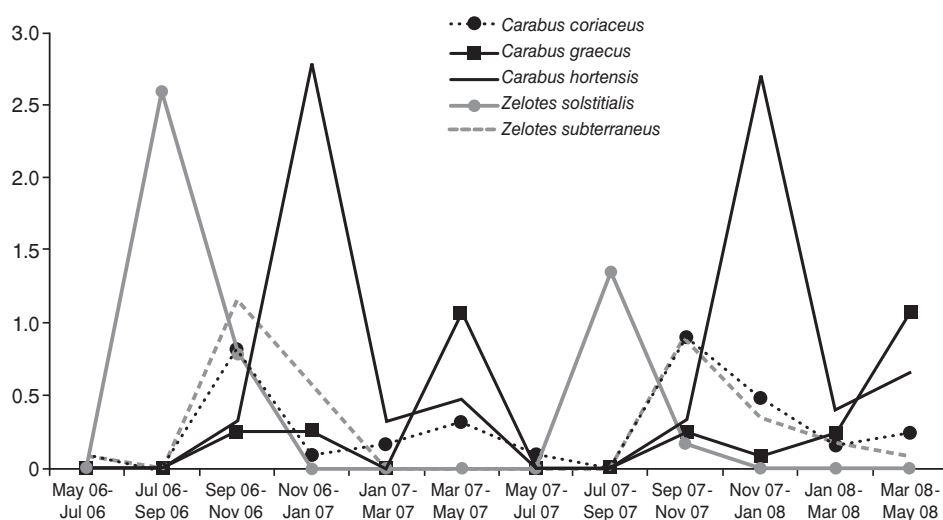


FIG. 3. Activity density (number of individuals per 100 trap-days) of dominant carabid species in Attiki (black) and gnaphosid species in Naxos (grey) per sampling period.

TABLE 5. Watson-William test results of pairwise comparison of median angles, respective to the mean period of maximal activity of each species

|                     | Pairs   | F      | <i>p</i>              |
|---------------------|---|--------|-----------------------|
| Carabidae (Attiki)  | <i>Carabus hortensis</i> – <i>Carabus graecus</i>         | 127.81 | $< 10^{-12}$          |
|                     | <i>Carabus hortensis</i> – <i>Carabus coriaceus</i>       | 11.98  | $6.59 \times 10^{-4}$ |
|                     | <i>Carabus graecus</i> – <i>Carabus coriaceus</i>         | 139.45 | $< 10^{-12}$          |
| Gnaphosidae (Naxos) | <i>Zelotes solstitialis</i> – <i>Zelotes subterraneus</i> | 198.57 | $< 10^{-12}$          |

Naxos (Rayleigh test:  $Z = 2.12$ ,  $p = 0.12$ ). The phenology of all species in significant pairs followed the von Mises distribution (Kuiper's test:  $p < 0.05$ ). The phenological patterns of *C. coriaceus* in Attiki slightly fluctuated between the two years of study, whereas *C. hortensis* and *C. graecus* exhibited strict phenologies (Fig. 3). Watson-William F-test showed that the activity patterns of species in all significantly segregated pairs differed temporally (Table 5). The abundance of *C. coriaceus* was maximal in October, *C. hortensis* was mostly active during December, whereas the abundance of *C. graecus* peaked during April. The phenology of *C. coriaceus* in Attiki was statistically different from its temporal activity in Samos ( $F = 24.632$ ,  $p = 1.49 \times 10^{-6}$ ), where it peaked during December. The temporal activity patterns of *Z. solstitialis* and *Z. subterraneus* in Naxos differed during both years of study (Watson William F-test:  $F = 196.441$ ,  $p < 10^{-12}$ ). Their abundance was maximal during late summer (mean vector: mid August) and mid autumn (mean vector: late October), respectively (Fig. 3).

#### Microhabitat preference and niche overlap

ANOSIM showed that the microhabitat preferences of ground beetles in Attiki differed significantly ( $R = 0.331$ ,  $p = 0.009$ ), especially between microhabitat ty-

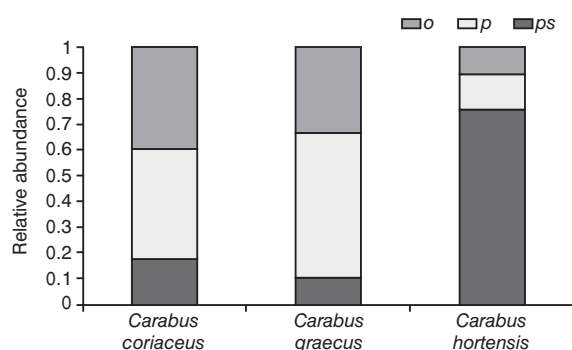


FIG. 4. Microhabitat preference of the three most abundant carabid species in Attiki. *ps*: dense vegetation with litter cover, *p*: scarce vegetation, *o*: open field.

pes *ps* and *p* ( $R = 0.56$ ,  $p = 0.024$ ) and *ps* and *o* ( $R = 0.525$ ,  $p = 0.02$ ), mainly due to *C. hortensis* (SIMPER: *ps*-*p*: 44.28%; *ps*-*o*: 42.65%). Microhabitat types *p* and *o* did not differ ( $p$ , *o*:  $R = -0.2$ ,  $p = 0.875$ ). The differentiation of microhabitat type *ps* was mainly due to the high abundance of *C. hortensis* there, compared to the other two species, which exhibited no microhabitat preference, but were least abundant in *ps* microhabitats (Fig. 4). No microhabitat differentiation of species was found for all other beetle and spider communities ( $-0.1 < R < 0.166$ ,  $0.125 < p < 0.935$ ).

Niche overlap of the three *Carabus* species in Attiki was lower than expected by chance (obs. mean = 0.284; sim. mean = 0.507; SES = -2.554;  $p = 0.007$ ). Pairwise analysis showed that niche overlap was minimum between *C. hortensis* and *C. graecus* (0.117). Low observed niche overlap compared to null expectation was found between *Z. solstitialis* and its congeneric *Z. subterraneus* in Naxos (obs. mean = 0.016; sim. mean = 0.161; SES = -1.117;  $p = 0.095$ ).

## DISCUSSION

### *Carabidae*

We found random patterns of co-occurrence at all sites, except Attiki, where carabid species proved to co-occur less than expected, and the observed C-score was significantly higher than expected by chance during the whole study and during each year separately (Table 2). This consistent segregational pattern represents a competitively structured community, as a result of deterministic processes (Gotelli & Graves, 1996). Segregational (Ulrich & Zalewski, 2006) as well as random co-occurrence patterns (Ulrich *et al.*, 2004) have arisen in previous studies on Carabidae. Even though the presence of competition in carabid communities is doubted (Loreau, 1990; Niemelä, 1993), the possibility of interspecific competition is higher for the dominant carabid species, whereas rarer, habitat specialist species are primarily influenced by abi-



otic factors (Loreau, 1992). This was affirmed by the spatiotemporal differentiation among the dominant carabid species in Attiki. These species led null models to statistical significance (contribution to most CU) and segregation was not random, but mainly a result of microhabitat differentiation between *Carabus hortensis* and its congeners *C. graecus*, *C. coriaceus* (Fig. 4), which generally have similar ecological preferences (Turin et al., 2003). Although competition may cause a shifting in the temporal activity of species with similar feeding habits (Loreau, 1990; Niemelä, 1993), it is not certain if differences in phenology are mechanisms of competition reduction or avoidance (Loreau, 1989). However, the remarkable phenological differences of *Carabus* species in Attiki (Table 5) and the statistically different patterns of *C. coriaceus* in Attiki and Samos indicate avoidance due to competition with *C. hortensis* in continental Greece.

The differentiation of microhabitat preference by congeneric carabid species is reported for the first time. The comparatively high abundance of *C. hortensis* in shaded, litter microhabitat (*ps*) contrary to its congeners *C. graecus* and *C. coriaceus* (Fig. 4), reflects a typical continental, equilibrium pattern, with increased competition intensity for resource utilization, compared to the lower biotic interactions in insular communities (Pianka, 2006).

The co-occurrence and body size overlap patterns of ground beetles in Crete and Cyprus were random. However, differential grazing pressure affected the assembly of carabid communities, as the body size-frequency distributions in relatively undisturbed sites were heavily left-skewed, contrary to overgrazed sites (Crete, Cyprus) (Table 4). Besides, based on the number of captures, all carabid populations in Cyprus were evidently sparse, contrary to the other four carabid communities. Low abundance of carabids in Cyprus (see online supplementary material, Table S1) was possibly caused by disturbance, though there is no direct evidence for this argument.

### *Gnaphosidae*

Body size overlap patterns proved to be random at all sites (Table 4), as well as assembly of ground spiders, except for a segregated pattern in Naxos, which was close to significance. These results were affirmed only for the second year of study, and tended towards aggregation during the first year (Table 2). This annual inconsistency of co-occurrence patterns, which indicates instability in the community, was due to the

annually different assembly of dominant species. *Pterotricha lentiginosa* and *Zelotes tenuis* were highly aggregated during the first year, while *Z. solstitialis* and *Z. subterraneus* were highly segregated during the second year of study. Thus, each of those pairs directed the whole assembly towards different annual co-occurrence patterns. The phenologies of the latter two species were significantly different (Table 5), affirming previous results (Chatzaki, 2003). Moreover, their niche overlap was lower than expected (although without reaching significance), hence indicating a possible, yet unconfirmed, competitive pattern between *Z. solstitialis* and *Z. subterraneus*.

The abundances, co-occurrence and body size overlap patterns of ground spiders show that, contrary to carabids, disturbance did not affect the spider communities. However, the body size-frequency distributions of gnaphosids in overgrazed sites (Crete, Cyprus) were heavily right-skewed, indicating the dominance of smaller species in Crete and Cyprus, as was also affirmed for carabids (Table 4). In previous studies, epigeal spiders proved to be affected by grazing pressure (Bell et al., 2001; Horváth et al., 2009) or not (Baudry & Asselin, 1991), exhibited segregational patterns (Ulrich et al., 2010), and proved to be good bioindicators of direct anthropogenic disturbance (Buchholz, 2010). Especially Gnaphosidae were sensitive to the disturbance caused by urbanization (Magura et al., 2010) and they were positively correlated with burnt habitats, assuming a preference towards more simplified and open territories by these spiders (Niwa & Peck, 2002). However, the influence of different regime and nature of disturbance on Gnaphosidae is still largely unknown. Further studies focused on family level are needed in order to include the natural history of species of such taxonomically wide and ecologically diverse family as Gnaphosidae (Chatzaki, 2003).

## CONCLUSIONS

Our research pointed out that increased disturbance partially affected the total abundance within communities or possibly led to a spatiotemporal segregation of co-occurring species. The annual consistency of co-occurrence patterns was generally higher for beetles and spiders in Attiki (continental area) and Samos (continental area until recently). Unusual patterns in the body sizes of coexisting species, differentiation of microhabitat preference and shifting in phenology among least co-occurring congeneric species denote

the potential of null models as a tool for revealing the interspecific relations within assemblages in a local scale. Regarding the eastern Mediterranean, where environmental conditions change rapidly and considerably, the relative weighting of diffuse competition and random dispersal in shaping assembly may help improve our knowledge on interspecific relations and compare communities in differential perturbation regimes with time being an explanatory factor.

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