

Overgrazed shrublands support high taxonomic, functional and temporal diversity of Mediterranean ground spider assemblages

Dimitris Kaltsas^{a,*}, Eleni Panayiotou^b, Konstantinos Kougioumoutzis^c, Maria Chatzaki^d

^a Don Daleziou 45, 382 21 Volos, Greece

^b Palagia Alexandroupolis, PO Box 510, 681 00 Alexandroupolis, Greece

^c Laboratory of Systematic Botany, Department of Crop Science, Agricultural University of Athens, Iera Odos 75, 118 55 Athens, Greece

^d Department of Molecular Biology and Genetics, Democritus University of Thrace, Dragana, 681 00 Alexandroupolis, Greece

ARTICLE INFO

Keywords:

Indicator species
Gnaphosidae
Crete
Maquis
Livestock grazing
Habitat degradation

ABSTRACT

The phryganic and maquis shrublands form the most typical vegetal formations in the Eastern Mediterranean that since thousands of years have been subject to various types of anthropogenic disturbance, including grazing. We studied the impact of sheep and goat grazing on 50 assemblages of ground spiders (Araneae: Gnaphosidae) in phryganic, maquis and forest habitats from zero to 2000 m elevation on Crete, Greece using pitfall traps for one year at each sampling site. In total, 58 gnaphosid species and 16,592 individuals were collected. Cretan endemic Gnaphosidae were negatively affected by intensive grazing and, contrary to findings on other taxa studied on the island, they were sparse and rare throughout the study area. The species composition of gnaphosid assemblages was primarily determined by elevation. *Trachyzelotes lyonnetai*, *Urozelotes rusticus*, *Zelotes scrutatus*, *Anagraphis pallens* and *Berinda amabilis* proved to be significant indicators of overgrazing. The vast majority of spiders belonging to synanthropic and nationally red-listed species were found in overgrazed sites. Despite theoretical expectations, while the average activity density decreased, the number of species, evenness, rarity, taxonomic, temporal and functional diversity (*FRic*) indices increased with increasing grazing intensity. This was mainly due to the nature of disturbance itself, which probably allows equilibrated low abundances of indigenous or synanthropic species, rather than overdominance of few, thus partly refuting the opportunistic species hypothesis (OSH). Ground spider assemblages in overgrazed sites comprised sparse populations of mostly rare, opportunistic species with different combinations of life-history traits that partly replace other species more commonly found in the less degraded sites. Species of these assemblages shorten their phenologies to minimize temporal co-occurrence with each other due to resource limitation. These distinct community patterns highlight ground spiders as good indicators of grazing pressure on Crete, on species and assemblage level. To conserve the indigenous and potentially endangered invertebrate fauna, the spatiotemporal discontinuity of grazing including rested patches is important in order to maintain spatial variability and possibly lead to habitat restoration.

1. Introduction

Most biotopes and ecotope types have been subject to anthropogenic disturbance for several millennia, which in most cases leads to loss of biological diversity (Ehrlich and Ehrlich, 1981). However, different ecotopes are differentially affected and their importance for conservation also varies. More specifically, Mediterranean shrublands are among the most biodiverse ecosystems in Europe (Verdú et al., 2000; Allen, 2003) and Mediterranean landscapes have been molded as a result of various human activities, mainly cultivation and grazing (Blondel, 2006). The extended – and until recently in many cases

uncontrolled – use of Mediterranean grasslands, shrublands, and forests as pastures has significantly altered the natural landscapes. Though moderate grazing may increase plant species richness in Mediterranean environments (Noy-Meir et al., 1989) by creating clearings where the competition is lower thus enhancing habitat diversity (Verdú et al., 2000), overgrazing ultimately leads to increased vegetation fragility and acceleration of soil degradation (Di Castri, 1981). Consequently, vegetation diversity and composition are influenced through reversal in succession or an increase in ruderal species (Tzanopoulos et al., 2007). In the Mediterranean region, overgrazing has been pernicious, causing a shift in the soil nutrient status which may result in decreased primary

* Corresponding author.

E-mail addresses: dimitris.kaltsas@gmail.com (D. Kaltsas), elen.panayiotou@gmail.com (E. Panayiotou), kkougiou@aia.gr (K. Kougioumoutzis), mchatzak@mbg.duth.gr (M. Chatzaki).

<https://doi.org/10.1016/j.ecolind.2019.04.024>

Received 9 January 2019; Received in revised form 6 April 2019; Accepted 9 April 2019

1470-160X/ © 2019 Published by Elsevier Ltd.

production and matches degradation, especially in cases of large increases in livestock numbers (Perevolotsky and Seligman, 1998).

Several locations in Crete, the largest island in Greece and fifth largest in the Mediterranean, represent characteristic cases of human induced land degradation, as well as decreasing vegetation cover and richness due to uninterrupted intensive grazing (Hill et al., 1998). Livestock grazing is an old, historically consistent human activity and an essential part of the ecosystems of Crete (Vogiatzakis and Rackham, 2008). However, its intensification during the last 50 years from the lowlands to high altitudes stems from deforestation and the dramatic increase of livestock numbers on the island (Lyrantzis, 1996). Today, insufficient grazing management leads to overgrazing in the lowlands, abandonment of lands on the inaccessible mountainous regions and long term productivity decline (Hadjigeorgiou et al., 2002). At low elevations, the natural arborescent evergreen sclerophyllous species have been extensively replaced by drought-deciduous shrubs, known as phrygana (*sensu* Di Castri, 1981) that cover most of the landscape, whereas only relict patches of indigenous forests still remain. At higher altitudes and more humid environments phrygana are gradually replaced by evergreen taller shrubs or small trees known as maquis. However, these two formations are sometimes intermixed (Rackham and Moody, 1996) into mosaic vegetation which is often related to intensive grazing (Vogiatzakis and Rackham, 2008). Phrygana, maquis and subalpine shrubs cover more than half of Crete and among others, they represent four habitat types (arborescent matorral with *Juniperus* spp., thermo-Mediterranean and pre-desert scrub, *Sarcopoterium spinosum* phryganas, endemic phrygana of the *Euphorbio-Verbascion*) included in Annex I of the Directive 92/43/EEC. Even though the monitoring importance of all four Natura 2000 habitat types has been ranked as high, they are nonetheless practically exposed to anthropogenic disturbance (Dimopoulos et al., 2006).

To assess the conservation status of these habitats, a primary monitoring study involves finding appropriate bioindicators to get a basis for further impact assessments. A thorough community level study may also reveal various consequences of disturbance, such as grazing, on spatiotemporal diversity and the patterns of assemblage composition (Kaltsas et al., 2013), since grazing causes the reduction of evenness and changes in the species composition of assemblages in many faunal groups (King and Hutchinson, 2007). Besides, functional diversity is expected to decrease at high disturbance levels when species are filtered out (Cornwell et al., 2006; Flynn et al., 2009). Similarly, the combination of life-history traits of co-occurrent species is expected to change under different disturbance regimes as the composition of assemblages is significantly altered. Given that changes in abundance distribution occur before local species extinction, reductions in functional diversity metrics incorporating abundance will reveal the impact of disturbance early, as they are better predictors of ecosystem processes than taxonomic diversity (Naeem et al., 2012; Mouillot et al., 2013).

Arthropods are important components of native ecosystems and ideal organisms for studying the effects of grazing because they respond to various types of disturbance faster than organisms with longer generation times (Niemelä et al., 1993) and in rapid numerical variations (Gerlach et al., 2013). Significant changes are reflected on communities of arthropods which are very diverse, abundant (Kremen et al., 1993; Bromham et al., 1999) and particularly good bioindicators because they are sensitive to local conditions due to their small size (Gerlach et al., 2013). In particular, groups with relatively low dispersal abilities, such as ground dwelling, non-flying taxa, are more sensitive to local habitat changes (Blaum et al., 2009). Nevertheless, arthropods had been neglected in conservation strategies until recently, and especially in the Eastern Mediterranean, invertebrate assemblages have rarely been studied as indicators of long-term land use (Kaltsas et al., 2012a, 2013).

Spiders are a model group for ecological studies and have been the focus of research on terrestrial communities since the early 1980s. They are very common in most habitat types and are good indicators of

environmental change, due to their ability to rapidly occupy habitats that have recently become favourable to them (Baudry and Asselin, 1991). Furthermore, ground dwellers are easily sampled in quantifiable ways (i.e. pitfall traps), and they form the most diverse arachnid group. Although spiders are exclusively carnivorous animals, they are greatly affected by the physical structure of environments (e.g. soil structure, density of vegetation) which influences their habitat preference and foraging success (Gibson et al., 1992) through changes in microclimate and prey availability (Bell et al., 2001), factors that may also be dependent on grazing effects (van Klink et al., 2016). Spiders are also suitable indicators of the wider effects of grazing on arthropods (Gibson et al., 1992), because they strongly influence local insect populations (Waloff, 1980). A meta-analysis by Prieto-Benítez and Méndez (2011) showed that land management and especially mechanical disturbances (ploughing, cutting and grazing) have negative effects on spider species richness, abundance and diversity at agroecosystems and rangelands due to negative effects on habitat heterogeneity or prey populations, but less at forests, where the main negative effect is fragmentation. Almost all of the studies focusing on the impact of grazing on spiders included several spider families with different life patterns and ecological requirements (e.g. ground wanderers, web-builders, arboreal spiders) (e.g. references in van Klink et al., 2016).

Herein, we focus on a single spider family, the ground spiders (Araneae: Gnaphosidae) to reveal the potential effects of livestock grazing on Crete, Greece within narrow taxonomic and functional space. Gnaphosidae is the sixth largest spider family in the world, including 2530 species and 158 genera (World Spider Catalog, 2018). In Greece, 148 species and 30 genera have been recorded (Chatzaki et al., 2015), constituting one of the most diverse and dominant spider families in terms of species richness (Chatzaki et al., 1998, 2005; Chatzaki, 2003; Chatzaki and Kaltsas, 2018) and relative abundance which may reach half the total annual abundance of the ground dwelling spider assemblages and up to 77% dominance during maximal activity (Chatzaki et al., 1998). Gnaphosid spiders are mostly epigean nocturnal predators that are best collected using pitfall traps, known to respond to anthropogenic disturbance in the Eastern Mediterranean (Kaltsas et al., 2012b, 2014). Their diversity and distribution in Crete are highly affected by elevation (Chatzaki et al., 2005). We investigated the following hypotheses: (i) the species composition of gnaphosid assemblages differs along altitudinal zones, habitat types and grazing levels, ii) spider communities in overgrazed sites include opportunistic species that only occur under high levels of disturbance (Bonte et al., 2000; Lyons et al., 2018), iii) spider taxonomic diversity and abundance are lowest in overgrazed sites (e.g. Gibson et al., 1992; Bromham et al., 1999; Dennis et al., 2001; Warui et al., 2005; Paschetta et al., 2013), while functional diversity does not change with grazing intensity due to the narrow functional space of co-familiar species.

2. Materials and methods

2.1. Study area

Crete covers 8336 km², 39% of which are above 400 m altitude, owing to the three limestone mountain massifs which include 58 summits over 2000 m: Lefka Ori in the western part, Psiloreitis in the central part and Lasithiotika Ori in the eastern part of the island. As in most Aegean islands, phrygana is the prevailing vegetation type throughout the island. These low scrubs often coexist with maquis species, forming patchy mosaic-like formations in several areas of the island. Forests are scarce, especially in the central and eastern part of Crete. *Pinus brutia* is the dominant woodland species and there are also *Cupressus sempervirens* formations (Rackham and Moody, 1996). The most dominant phryganic species at low elevations are *Thymra capitata*, *Sarcopoterium spinosum*, *Genista acanthoclada*, *Calicotome villosa*, *Phlomis fruticosa*, *Cistus salvifolius*, *Euphorbia acanthothamnus* and *Bal-lota pseudodictamnus*. Maquis species which dominate mainly at

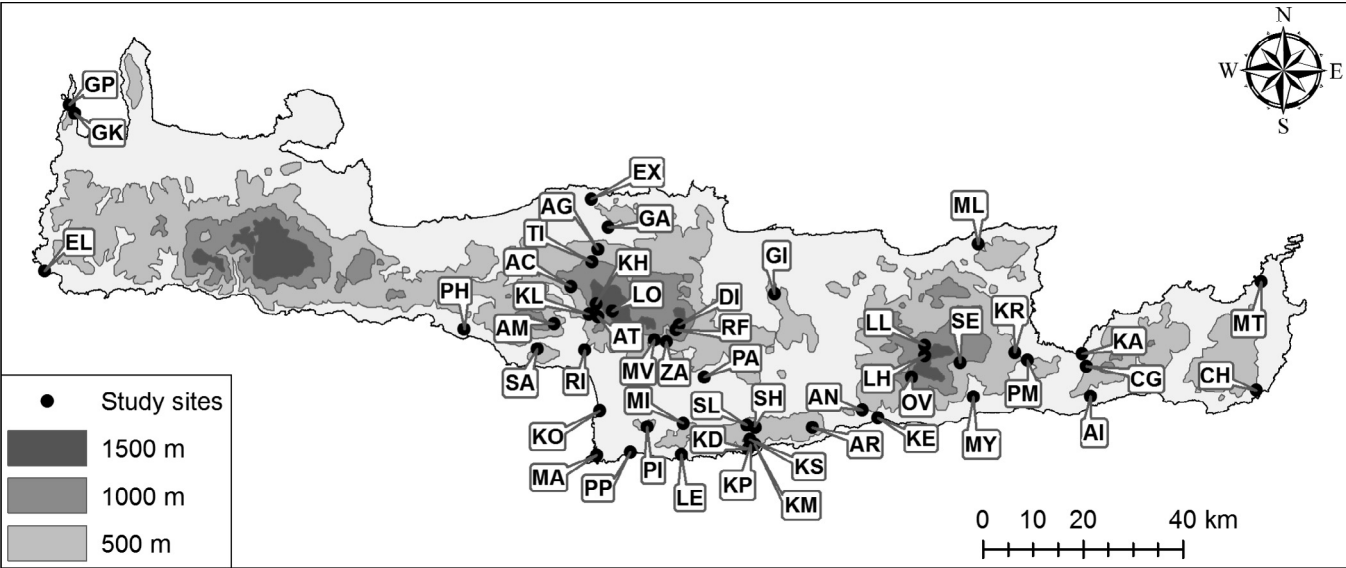


Fig. 1. Localities of the 50 study sites in Crete. Study site characteristics and details on samplings in Appendix A.

intermediate altitudes are *Pistacia lentiscus*, *Juniperus phoenicea*, *Quercus coccifera*, *Arbutus unedo*, *Ceratonia siliqua* and *Euphorbia dendroides*. Subalpine shrubs, which may exceed the timberline, include *Berberis cretica*, *Rhamnus saxatilis* and *Astragalus angustifolius*.

2.2. Sampling design and taxonomic identification

Overall, 50 study sites were sampled, ranging from the northern part of Crete (e.g. GP) to the southernmost coasts to the Libyan Sea (e.g. MA, PP, LE), from the western (EL, GP, GK) to the eastern end of Crete (MT, CH), and from almost zero altitude near the coasts of the island (e.g. EL, KE, KO, LE, PP) up to high elevations in Psiloritis (KH, LO) and Dikti (LH, LL) mountains (Fig. 1). We did not include Lefka Ori mountain-range in our study because of great spatial disruption between sites of zero and low altitudes (not belonging to the same mountain massif) and subsequent zones. All sampling sites were located within areas with natural vegetation, away from cultivations and urban regions. The study sites were grouped into four altitudinal zones, based on the altitudinal arrangements proposed by Qu  zel and Barbero (1982) and five different habitat types were distinguished (Table 1).

Table 1
Altitudinal zones, habitat types and theoretical grazing levels of the 50 study sites in Crete.

Factor	Class	Description	Number of sites
Altitude	ALT1	(0–399 m) – thermo-mediterranean zone	23
	ALT2	(400–699 m) – meso-mediterranean zone	13
	ALT3	(700–1599 m) – supra-mediterranean zone	11
	ALT4	(1600–2199 m) – montane Mediterranean zone	3
Habitat	CP	coastal phrygana	9
	IP	inland phrygana	25
	M	maquis	10
	PF	pine forests	2
	SS	subalpine shrubs	4
Grazing	G0	no grazing (< 1% coverage of human impact indicators)	0
	G1	occasional/rare grazing (1–5% coverage)	0
	G2	low grazing intensity (5–25% coverage)	10
	G3	intermediate grazing (25–50% coverage)	14
	G4	intense grazing (50–75% coverage)	17
	G5	overgrazing/degradation due to grazing (75–100% coverage)	9

The habitat type of each sampling site refers to the dominant vegetation, e.g. both pine forests (PF) in our study also include maquis species. The grazing level at each study site was assessed by identifying and recording indicator plant species of human-induced disturbance and specifically grazing, such as *Asphodelus aestivus*, *Drimys maritima*, *Phlomis cretica*, *P. lanata*, *P. fruticosa* and *Onopordum* spp. (Horvat et al., 1974; Papanastasis and Noitsakis, 1992). The cover of these species was measured using the Braun-Blanquet method and six theoretical levels of grazing pressure were distinguished following Kaltsas et al. (2013) (Table 1). No sites were grouped into G0 and G1 classes (Appendix A), because generally or relatively ungrazed areas are very scattered in Crete and none was identified as such. The livestock in Crete are herds of sheep and goats (mainly the latter).

The samplings included here are part of a wide sampling net throughout Crete carried out by staff of the Natural History Museum of Crete during the late 90s. Part of them were also included in a study of Gnaphosidae along altitudinal gradients in Crete, which however, did not incorporate habitat specialization and disturbance effects (Chatzaki et al., 2005) and in a more recent study on the impact of grazing on ground beetles (Kaltsas et al., 2013). Samples were collected using pitfall traps, which were plastic containers 12 cm tall, 9.5 cm diameter at the top, one-quarter filled with ethylene glycol and placed flush with the ground surface. The sampling protocol was the same at all sampling sites. The 15–20 traps set in every site (inter-trap distance: 10–20 m) were changed at two months intervals and samplings lasted for one year at all study sites starting from late May 1996 to early May 2000 (Appendix A). Some spider species were classified as synanthropic based on bibliographic data regarding their habitat preference and their distribution. Spider samples were preserved in 96% ethanol and Gnaphosidae specimens were identified to species level. The nomenclature follows the World Spider Catalog (2018). The material is deposited in the Araneae collection of the Natural History Museum of the University of Crete.

2.3. Data analysis

Species richness for each study site was estimated as the average of three nonparametric, incidence-based estimators: Chao1, Jackknife1 and Bootstrap (detailed description in Colwell, 2013). The observed number of species (*S*) was divided by the average expected number of species and a minimum of 75% was set as the lower limit of sampling completeness. We also tested the asymptotic level of the respective

accumulation curves, by measuring the final slope of each curve, setting the score of 0.04 as the threshold for sampling adequacy (Kaltsas et al., 2013). Richness estimations and accumulation curve data were based on the mean of 100 randomizations using EstimateS 9.1.0, (Colwell, 2013). Spider communities which proved to be undersampled were excluded from all diversity analyses.

The diversity of adequately sampled communities was calculated through i) Simpson's evenness index: $1 - D = \sum_i (n_i/n)^2$ where n_i is the number of individuals of taxon i , and n is the total number of individuals of a community in a given site and ii) Effective Number of Species (ENS), the 'true diversity' index by Jost (2006) which expresses the number of equally abundant species that obtain the same mean proportional species abundance as that in a real assemblage. The temporal diversity of spider communities (β_t) was measured as the proportion of exclusive species to total species richness between consecutive sampling periods, i.e. the temporal change of community composition. β_t was calculated for each assemblage using the complementarity index of Colwell and Coddington (1994): $C_{jk} = [(S_j + S_k - 2V_{jk}) / (S_j + S_k - V_{jk})] \times 100$, where S_j is the number of species in sampling period j , S_k the number of species in consecutive sampling period k ($k = j + 1$) and V_{jk} the common species in periods j and k . C_{jk} was calculated for consecutive sampling periods and β_t was calculated as the average for each community. Species rarity was calculated as: $1 - m_i/m$, where m_i is the number of sites where species i was found and m is the total number of sites ($m = 50$). The total rarity for each sampling site was calculated as: $R = \sum_{i=1}^S (a_i/a)(1 - m_i/m)$, where a_i is the activity density of species i , a is the total activity density of all captured species at each site, and S is the total number of species captured at each sampling site. We also calculated three functional diversity metrics introduced by Villéger et al. (2008): a) *FRic* (functional richness), which is the amount of niche space filled by species in a community i.e. the volume of a convex hull around the species of a community projected in trait space, b) *FEve* (functional evenness), which measures the regularity of species' abundances in functional space, and c) *FDiv* (functional divergence), a measure of the degree to which the abundance distribution of an assemblage maximizes functional trait differences. *FEve* and *FDiv* integrate the relative abundances of species. Gnaphosid species were assigned to five life-history traits: average body length of females, distribution range, period of peak activity, elevational range, and prey range. Data was assessed based solely on literature (distribution range, prey range) or on literature and personal data (the other three traits) (details in Appendices C, D). The three functional diversity indices were calculated using the 'dbFD' function in the 'FD' package (Laliberté et al., 2014) in the statistical language R version 3.4.4 (R Development Core Team, 2018).

The total activity densities, species richness, diversity metrics and rarity of adequately sampled sites were compared among different factor classes (grazing, altitude, habitat types) using one-way ANOVA or Kruskal-Wallis test (post hoc analyses were performed through Tukey's test and Mann-Whitney's test, respectively). The normality of data was tested with the Shapiro-Wilk test. Possible significant patterns of the aforementioned variables (activity density, S , H' , $1-D$, β_t , R , *FRic*, *FEve*, *FDiv*) with altitude (continuous variable) were tested using linear and polynomial regression (based on the highest R^2).

The compositional differences of the 50 study sites in relation to altitude, habitat and grazing level was detected using Multiple Response Permutation Procedure (MRPP), a nonparametric permutation method that can test the probability of difference between two or more groups against the null hypothesis of no difference. Average within group dissimilarity was estimated based on the Bray-Curtis distance measure. MRPP calculates the T statistic which expresses the difference between two groups (lower T values indicate more different groups) as well as the A statistic which describes the homogeneity within groups and ranges from 0 (random structure) to 1 (the species and their respective abundances are identical) (McCune et al., 2002). In order to maintain significance levels of $\alpha = 0.05$, we used a

Bonferroni-corrected critical value. The differences among gnaphosid site assemblages in different ecological or geographical groups were visualized with Non-Metric Multidimensional Scaling (NMDS) based on the Bray-Curtis dissimilarity matrix. Possible correlations between factors (altitudinal zones, grazing levels and habitat types) were detected with the chi-square test of independence. Indicator Species Analysis (ISA) was applied to test for potential indicators, setting the level of grazing, altitudinal zone or habitat type as the grouping variable. ISA 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). Statistical significance was tested compared to the average of 4999 permutations. We included all species represented by more than 20 individuals in total (Kaltsas et al., 2013). The maximum value of IndVal is 100, when all individuals of a species are solely captured at all sites of one specific factor class. MRPP and ISA were performed in PC-ORD 6.04 (McCune and Mefford, 2011). ANOVA and NMDS were applied in PAST version 2.15 (Hammer et al., 2001).

3. Results

3.1. Composition of assemblages

Overall, we identified 58 gnaphosid species (16.4 ± 3.8 per site) and 26 genera (10.9 ± 2 per site) in a total of 16,592 individuals (Appendix B). The most abundant species was *Pterotricha lentiginosa* (25.8% of the total gnaphosid activity density) followed by *Zelotes subterraneus* (12.5% of the total activity density) and these two species were also the commonest throughout the study area, being present at all but one single site (KO). Most of the total activity density of *P. lentiginosa* (39.9%) was recorded at G2 sites, more than the sum of its activity density at G4 and G5 sites (38.8%) (percentages after equally weighting grazing levels), and differed significantly among grazing levels G2 and G5 (Kruskal-Wallis ANOVA: $H = 11.45$, d.f. = 3, $p = 0.01$). Overall, nine species are Greek endemics among which six are Cretan endemics, six species are synanthropic (*Drassodes serraticheilis*, *Heser nilicola*, *Trachyzelotes barbatus*, *T. lyonneti*, *Urozelotes rusticus*, *Zelotes laetus*), and four of them are included in the Red Data Book of threatened animals of Greece (Legakis and Maragou, 2009) (Appendix B). Most of the activity density of Cretan endemic species was recorded at G3 (42.69%) and G2 sites (32.22%) (Fig. 2), while their average rarity

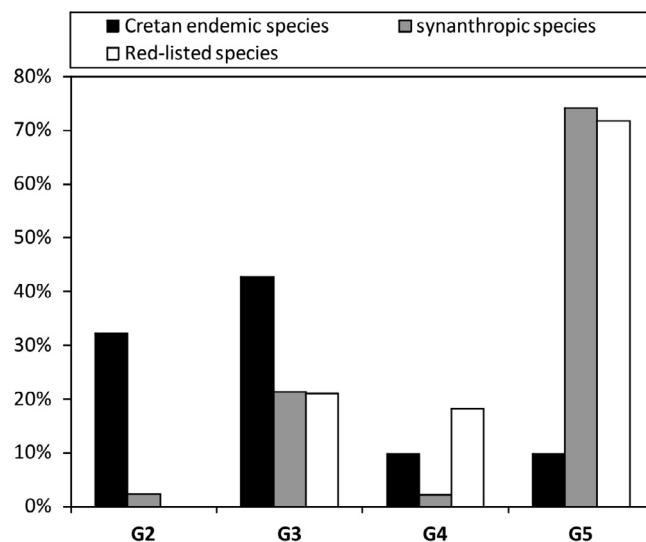


Fig. 2. Percentage of activity density of synanthropic and Cretan endemic gnaphosid species (Appendix B) under different grazing levels in Crete. The percentages were equally weighted due to the different number of sites in G2, G3, G4 and G5.

Table 2

Sampling adequacy results for the 50 study sites. Estimated species richness *S* and sampling completeness (%) are based on the average of Chao1, Jackknife1 and Bootstrap richness estimators. Slope: the final slope of each accumulation curve as a measure of its asymptotic level. The sites with a sampling completeness lower than 75% and/or a slope higher than 0.04 were considered as undersampled (bold characters).

Code	Species	Estimated <i>S</i>	Singletons (%)	Doubletons (%)	Sampling completeness (%)	Slope
AC	23	27	4.35	8.70	85.185	0.022
AG	21	27	33.33	9.52	77.778	0.031
AI	12	18.45	50.00	8.33	65.041	0.250
AM	19	24.28	21.05	10.53	78.261	0.032
AN	18	22	27.78	11.11	81.818	0.060
AR	21	23	14.29	14.29	91.304	0.014
AT	15	19	26.67	13.33	78.947	0.086
CG	16	20	31.25	25.00	80.000	0.159
CH	17	20.58	11.77	47.06	82.604	0.060
DI	15	18	33.33	13.33	83.333	0.014
EL	18	19	11.11	5.56	94.737	0.010
EX	17	20	17.65	0.00	85.000	0.010
GA	16	20	18.75	0.00	80.000	0.042
GI	12	13	16.67	0.00	92.308	0.005
GK	19	22	15.79	5.26	86.364	0.020
GP	20	25	30.00	10.00	80.000	0.021
KA	15	19	33.33	26.67	78.947	0.072
KD	15	16.07	13.33	6.67	93.333	0.010
KE	15	17	6.67	13.33	88.235	0.020
KH	14	16	14.29	14.29	87.500	0.010
KL	20	22	10.00	5.00	90.909	0.014
KM	12	14	25.00	8.33	85.714	0.015
KO	17	20.27	17.65	11.77	83.868	0.029
KP	11	11.93	9.09	9.09	92.205	0.008
KR	12	14	16.67	16.67	85.714	0.029
KS	16	17	6.25	31.25	94.118	0.010
LE	14	15.26	7.14	14.29	91.743	0.014
LH	7	7	0.00	14.29	100.000	0.005
LL	15	16	0.00	6.67	93.750	0.009
LO	9	9.43	0.00	0.00	95.440	0.002
MA	14	16	21.43	14.29	87.500	0.017
MI	22	26.53	22.73	18.18	82.925	0.059
ML	19	22	26.32	5.26	86.364	0.018
MT	14	15	0.00	7.14	93.333	0.014
MV	19	21	15.79	10.53	90.476	0.021
MY	17	20	23.53	17.65	85.000	0.069
OV	18	21	22.22	5.56	85.714	0.009
PA	23	27	21.74	4.35	85.185	0.013
PH	21	25.78	19.05	9.52	81.458	0.039
PI	15	17	20.00	6.67	88.235	0.012
PM	11	14	45.46	9.09	78.571	0.030
PP	11	13	27.27	9.09	84.615	0.031
RF	14	15	7.14	7.14	93.333	0.006
RI	22	27	27.27	9.09	81.481	0.020
SA	21	26.2	28.57	9.52	80.153	0.018
SE	22	27.24	31.82	13.64	80.769	0.039
SH	13	13	7.69	7.69	100.000	0.004
SL	18	22	27.78	5.56	81.818	0.016
TI	19	22	10.53	10.53	86.364	0.020
ZA	18	26	33.33	0.00	69.231	0.016

was 0.83 ± 0.14 (all other species: 0.7 ± 0.32). On the other hand, most of the activity density of synanthropic Gnaphosidae (74.14%) was recorded at overgrazed sites (G5) (Fig. 2) and differed significantly among grazing levels (Kruskal-Wallis ANOVA: $H = 9.34$, d.f. = 3, $p = 0.025$) mainly due to the significant differences of G5 with all other grazing levels (Mann-Whitney test: $0.008 < p < 0.025$). Among these species, *H. nilicola*, *U. rusticus* and *Z. laetus* were found only in G5 sites. In total, few individuals of all four endangered species were captured and most were captured at G5 sites (71.8% of activity density) (Fig. 2).

Chi-square test showed that altitudinal zone and habitat type were strongly dependent (chi-square = 49.87, d.f. = 12, $p < 0.001$), mainly due to the fact that all ALT4 study sites were subalpine shrublands (Appendix A), a habitat type defined by elevation. On the contrary, altitudinal zone and grazing level as well as grazing level and habitat type were independent (chi-square test: $p > 0.05$). After estimating sampling completeness and the asymptotic level of accumulation curves for the 50 study sites, we found that 10 sites did not fulfill at least one of

the two criteria of sampling adequacy and thus proved to be under-sampled (Table 2).

MRPP showed that the species composition of gnaphosid assemblages differed significantly across altitudinal zones and habitat types especially due to the specialized gnaphosid fauna at high altitudes (ALT4). On the other hand, it did not differ among grazing levels (Table 3). The altitudinal zonation of gnaphosid assemblages, especially regarding altitudinal zones ALT1 and ALT4, is shown in the NMDS 2D plot (Fig. 3) which explained 79% of the total variance (Axis 1: 54.9% of variance, Axis 2: 24.1% of variance, stress = 0.206). Gnaphosid communities at lower elevations (ALT1) were more structurally variant, the assemblages at ALT2 shared similarities with those at ALT3, and the three assemblages at higher altitudes (ALT4) were very similar in composition. The altitudinal zonation of gnaphosid assemblages was mainly due to the fact that some species were solely found at very high or low elevations. Specifically, ISA showed that the significant differences of assemblages were mainly due to the high activity density and

Table 3

MRPP results on differences in gnaphosid assemblage structure between altitudinal zones, habitat types and grazing levels (details in Table 1). Significant pairwise comparisons are Bonferroni-corrected.

Factor (classes)	T	A	p
Altitudinal zone	−6.187	0.143	< 0.0001
(ALT1 vs ALT3)	−7.048	0.130	0.0006
(ALT1 vs ALT4)	−5.497	0.135	0.0010
Habitat type	−3.281	0.089	0.0038
(CP vs SS)	−4.887	0.225	0.0085
Grazing level	0.410	−0.009	0.6153

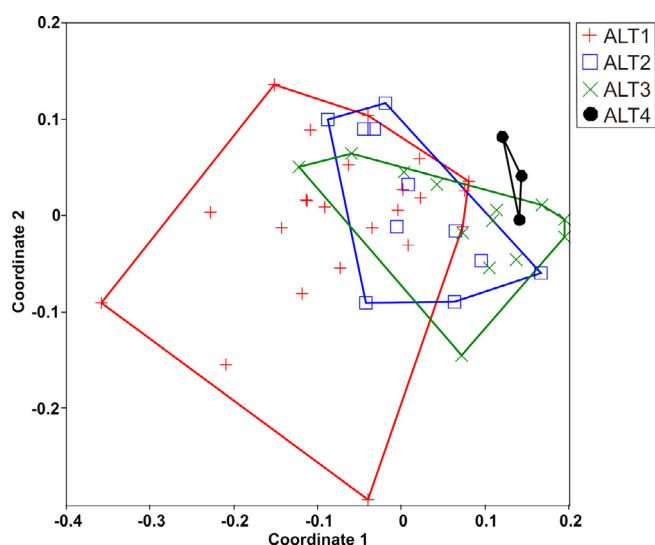


Fig. 3. NMDS 2D ordination plot of the site assemblages in the altitudinal zones using the Bray–Curtis dissimilarity matrix.

wide presence of *Drassodes albicans* and *Gnaphosa bithynica* at the ALT4 zone, and *Drassodes lapidosus* and *Drassyllus praeficus* at the ALT3 zone. *Pterotricha lentiginosa*, the most abundant gnaphosid species on Crete, as well as *Callilepis cretica*, one of the commonest species in our study, were among the few species that were frequent and highly abundant in subalpine shrublands (Table 4). On the contrary, several common and highly abundant species (*Anagraphis pallens*, *Zelotes babunaensis*, *Z. prishutovae*, *Z. scrutatus*, *Z. subterraneus*) were 1.5–7.7 times less abundant in mid and high (ALT3–4) elevations compared to ALT1–2. Besides, several gnaphosid species were captured more or exclusively in overgrazed sites. ISA showed that *Zelotes scrutatus*, *Anagraphis pallens*,

Table 4

ISA results (*sensu* Dufrêne and Legendre, 1997) on the species responsible for the significant differences among altitudinal zones, habitat types and grazing levels. IndVal: the indicator value for each species in a factor class.

Factor	Species	Group	Observed IndVal	Mean simulated IndVal \pm SD	p
Altitudinal zone	<i>Drassodes albicans</i>	ALT4	94.9	14.9 \pm 9.28	0.0008
	<i>Drassodes lapidosus</i>	ALT3	76.9	23.6 \pm 10.32	0.0020
	<i>Gnaphosa bithynica</i>	ALT4	66.7	10.0 \pm 8.02	0.0032
	<i>Drassyllus praeficus</i>	ALT3	47.2	27.9 \pm 9.53	0.0462
Habitat type	<i>Drassodes albicans</i>	SS	95.7	16.5 \pm 9.89	0.0004
	<i>Callilepis cretica</i>	SS	53.3	27.1 \pm 11.02	0.0300
	<i>Gnaphosa bithynica</i>	SS	50.0	12.5 \pm 8.39	0.0068
	<i>Pterotricha lentiginosa</i>	SS	43.3	31.8 \pm 5.64	0.0446
Grazing level	<i>Zelotes scrutatus</i>	G5	57.1	30.8 \pm 5.65	0.0006
	<i>Drassyllus praeficus</i>	G4	49.8	25.2 \pm 7.14	0.0070
	<i>Anagraphis pallens</i>	G5	40.4	29.2 \pm 4.84	0.0272
	<i>Trachyzelotes lyonnetai</i>	G5	39.7	18.4 \pm 8.13	0.0172
	<i>Berinda amabilis</i>	G5	33.8	16.4 \pm 6.98	0.0246
	<i>Urozelotes rusticus</i>	G5	22.2	9.8 \pm 4.01	0.0296

Trachyzelotes lyonnetai, *Berinda amabilis* and *Urozelotes rusticus* were significant indicators of overgrazing (G5 sites) and *D. praeficus* was a significant indicator of intensive grazing (G4 sites) (Table 4). Even though the activity density of the most abundant species, *P. lentiginosa*, differed significantly among grazing levels, the species was not a significant indicator of low grazing (G2: IndVal = 37.9, p = 0.176).

3.2. Richness and diversity patterns

Species richness was generally high at lower and intermediate altitudes (ALT1–3) (average: 10.15 ± 1.8 – 11 ± 2.2) and was lowest at ALT4 sites (7.0 ± 2.0), even though the quadratic equation relating (estimated) species richness with altitude was not significant. In total, 50 species were captured in the ALT1 zone, 43 in ALT2, 37 in ALT3 and only 17 in ALT4.

The significant differences in species richness and other diversity metrics with altitudinal zones, habitat type and grazing level as well as the post hoc significant results are shown in Table 5. The effect of grazing on all diversity metrics was further visualized in Fig. 4. To further avoid intermixing results on the effect of grazing by the effect of altitude, the same metrics were also calculated after excluding all ALT4 sites (significant pairs in parenthesis in Table 5 and black bars in Fig. 4). Except for species richness, no other diversity metric had any significant difference with altitude, either with linear or polynomial regression. Species richness and temporal diversity significantly differed among habitat types. In contrast, most of the metrics examined were found to be significantly affected by grazing level, with the exception of activity density and the functional metrics of evenness and divergence. However the difference of activity density between G2 and G5 proved to be significant, also after the exclusion of ALT4 sites (one-way ANOVA: $F = 8.77$, d.f. = 1, $p = 0.014$). Species (1-D) and functional evenness (*FEve*) were not highly correlated (Pearson's $r = 0.26$, $p = 0.107$).

4. Discussion

4.1. Composition of assemblages

In our study, 58 of the 72 Gnaphosidae species present on Crete were recorded; all 14 species not found in our study are uncommon or very rare on the island (Chatzaki et al., 2015). However, our findings include numerous additions to the distribution of most species on Crete, the most significant being the very rare *D. unicolor*, *H. minor*, *H. nilicola*, *P. senilis*, *U. rusticus* and *Z. laetus* and the four red-listed gnaphosid species of Greece (*C. creticus*, *L. manolisi*, *S. trichopus*, *Z. minous*) (Legakis and Maragou, 2009) which were all captured in our study

Table 5

One-way ANOVA (factors: S, A.D., ENS, FEve, FDiv) and Kruskal-Wallis ANOVA (factors: 1-D, βt , R, FRic) results and post hoc analyses (Tukey's test and Dunn's test respectively). Results in parentheses are after exclusion of ALT4 sites. S: species richness, A.D.: activity density, ENS: Effective Number of Species, 1-D: Simpson index, βt : temporal diversity, R: rarity index, FRic: functional richness, FEve: functional evenness, FDiv: functional divergence. p values of pairwise post hoc analyses: 0.001 < ** < 0.01 < * < 0.05.

One-way ANOVA	Variable	F	d.f.	p	post hoc (Tukey's test)
Altitudinal zone	S	3.73	3	0.0176	ALT1-ALT4**, ALT2-ALT4**, ALT3-ALT4**
	A.D.	1.18	3	0.1762	
	ENS	1.17	3	0.3354	
	FEve	0.77	3	0.5160	
	FDiv	0.77	3	0.5206	
Habitat type	S	5.42	4	0.0012	IP-SS*
	A.D.	1.31	4	0.2859	
	ENS	2.07	3	0.1061	
	FEve	1.46	3	0.2368	
	FDiv	1.33	3	0.2800	
Grazing level	S	4.52 (3.27)	3 (3)	0.0073 (0.0306)	G2-G5*, G2-G4* G2-G5*, G2-G4*
	A.D.	0.95 (1.06)	3 (3)	0.4288 (0.3778)	
	ENS	4.01 (2.98)	3 (3)	0.0146 (0.0453)	G2-G5* G2-G5*
	FEve	1.44 (0.19)	3 (3)	0.2461 (0.9006)	
	FDiv	0.22 (0.69)	3 (3)	0.8788 (0.5672)	
Kruskal-Wallis ANOVA	Variable	H	d.f.	p	post hoc (Mann-Whitney test)
Altitudinal zone	1-D	3.20	3	0.3616	
	βt	6.27	3	0.0991	
	R	1.27	3	0.7357	
	FRic	4.60	3	0.2035	
Habitat type	1-D	3.83	3	0.2806	
	βt	10.42	3	0.0153	CP-SS**, IP-SS**
	R	5.45	3	0.1416	
	FRic	6.65	3	0.0839	
Grazing level	1-D	11.12 (9.39)	3 (3)	0.0111 (0.0245)	G2-G5**, G2-G4**, G2-G3* (G2-G5*, G2-G4*)
	βt	20.56 (17.76)	3 (3)	0.0001 (0.0005)	G2-G5**, G3-G5**, G2-G4*, G4-G5*, G2-G3* (G2-G5**, G3-G5**, G2-G4*, G4-G5*)
	R	13.55 (14.94)	3 (3)	0.0036 (0.0019)	G2-G5*, G2-G4*, G3-G5*, G4-G5*, G2-G3* (G2-G5*, G2-G4*, G3-G5*, G4-G5*, G2-G3*)
	FRic	8.85 (6.64)	3 (3)	0.0314 (0.0843)	G2-G5*, G3-G5*

(Appendix B).

Our results show that the species composition of gnaphosid assemblages was primarily determined by the altitudinal zonation of the island, thus partly confirming our first hypothesis. The distribution of Gnaphosidae species was influenced by the significantly inter-correlated altitude and habitat type, especially regarding the structural differences of assemblages at subalpine shrublands and coastal phrygana and the respective elevational zones (ALT4 and ALT1). In line with Chatzaki et al. (2005), our results intensify the recognition of four altitudinal groups of Gnaphosidae based on their altitudinal range of distribution, as a result of the tolerance degree and/or adaptation of many species to temperature extremes, but also of the special palaeogeographic conditions under which this fauna evolved (details in Chatzaki et al., 2005): a) lowland species that are rare or absent at mid and high elevations, (e.g. *A. pallens*, *Z. babunaensis*, *Z. prishutovae*, *Z.*

scrutatus, *Z. subterraneus*), b) species widely distributed, mainly present at high elevations (e.g. *D. lapidosus*, *D. praeficus*), c) few species which are very abundant and exclusively present at very high elevations (*D. albicans*, *G. bithynica*) and d) species very common throughout the island, but also dominant above 1600 m (*P. lentiginosa*, *C. cretica*). This grouping of species along with the decreasing total number of species captured from ALT1 to ALT4 explain the variation in assemblage composition of lowland sites, the high degree of similarity among the three ALT4 sites (Fig. 3), and the significant differences between ALT1-ALT3 and ALT1-ALT4 (Table 3).

The composition of gnaphosid assemblages did not change statistically with grazing, contrary to previous studies which were centered on several spider families (Gibson et al., 1992; Churchill and Ludwig, 2004; Warui et al., 2005; Ford et al., 2012; Szinetár and Samu, 2012; Paschetta et al., 2013; Leroy et al., 2014; van Klink et al., 2016; Lyons et al., 2018). However, some remarks on qualitative variation among grazing levels are worth mentioning. For example, Cretan endemic species were more numerous in sites of lower grazing when compared to sites under intensive grazing (G4, G5) (Fig. 2), corroborating Paschetta et al. (2013) who found highest endemic spider richness under light grazing at areas with high plant diversity. The distribution of the Cretan endemic gnaphosid species recorded in our study was generally narrow and their populations rather small, as they were rarer in average than all other species and their activity density was particularly low. This contrasts with Cretan endemic species patterns of other arthropod groups such as carabid beetles (Kaltsas et al., 2013) and non-cavernicolous Chilopoda (Simaiakis et al., 2005) which are widely distributed and abundant in all habitat types of Crete, including overgrazed sites. On the other hand, the synanthropic species were even rarer and less abundant than the Cretan endemic species, and also significantly more abundant or exclusively present in overgrazed sites, confirming our second hypothesis. *H. nilicola*, *U. rusticus* and *Z. laetus* were found for the first time in natural habitats in Greece. The latter two had recently been recorded for the first time on Crete, in the centre and suburban areas of Heraklion city (Kaltsas et al., 2014). According to our results, *T. lyonneti*, *U. rusticus*, *Z. scrutatus*, *A. pallens* and *B. amabilis* are significant indicators of overgrazing and *D. praeficus* an indicator of intensive grazing on Crete (Table 4), showcasing *U. rusticus* as a general indicator of anthropogenic disturbance, since it had also proved to be a significant indicator of high levels of urbanization (Kaltsas et al., 2014).

4.2. Richness and diversity patterns

Quantitative data of assemblages at each grazing level revealed that average species richness increased significantly from G2 to G4 and G5 sites (Table 5), while the activity density was significantly higher in G2 than in G5 sites, regardless of altitude. Most previous studies have shown that total spider richness decreases with increasing grazing intensity (Gibson et al., 1992; Downie et al., 1999; Dennis et al., 2001, 2015; Warui et al., 2005; Pétilon et al., 2007; Szinetár and Samu, 2012; Paschetta et al., 2013) or is unaffected by grazing (Bromham et al., 1999; Harris et al., 2003; Lubin et al., 2011; Ford et al., 2012; Leroy et al., 2014; Zakkak et al., 2014). An increase in the number of spider species and/or abundance under high levels of grazing has been reported only for Linyphiidae (Gibson et al., 1992; Ford et al., 2012; van Klink et al., 2016) which can easily disperse by aerial 'ballooning' into disturbed habitats where competition from larger invertebrate predators is lower (Bell et al., 2001). However, the opposite has been found for ground dwellers in general (Fuller et al., 2014) and Gnaphosidae in particular (Churchill and Ludwig, 2004; Paschetta et al., 2013), which disperse energetically, hence much less, they are more abundant at heterogeneous habitats and more demanding in terms of microclimatic requirements (Paschetta et al., 2013). Spiders avoid adverse temperatures and desiccation at overgrazed pastures by finding shelter into tall vegetation patches which are better provided in pastures grazed by cattle rather than by sheep (De Keer et al., 1989), let alone goats which

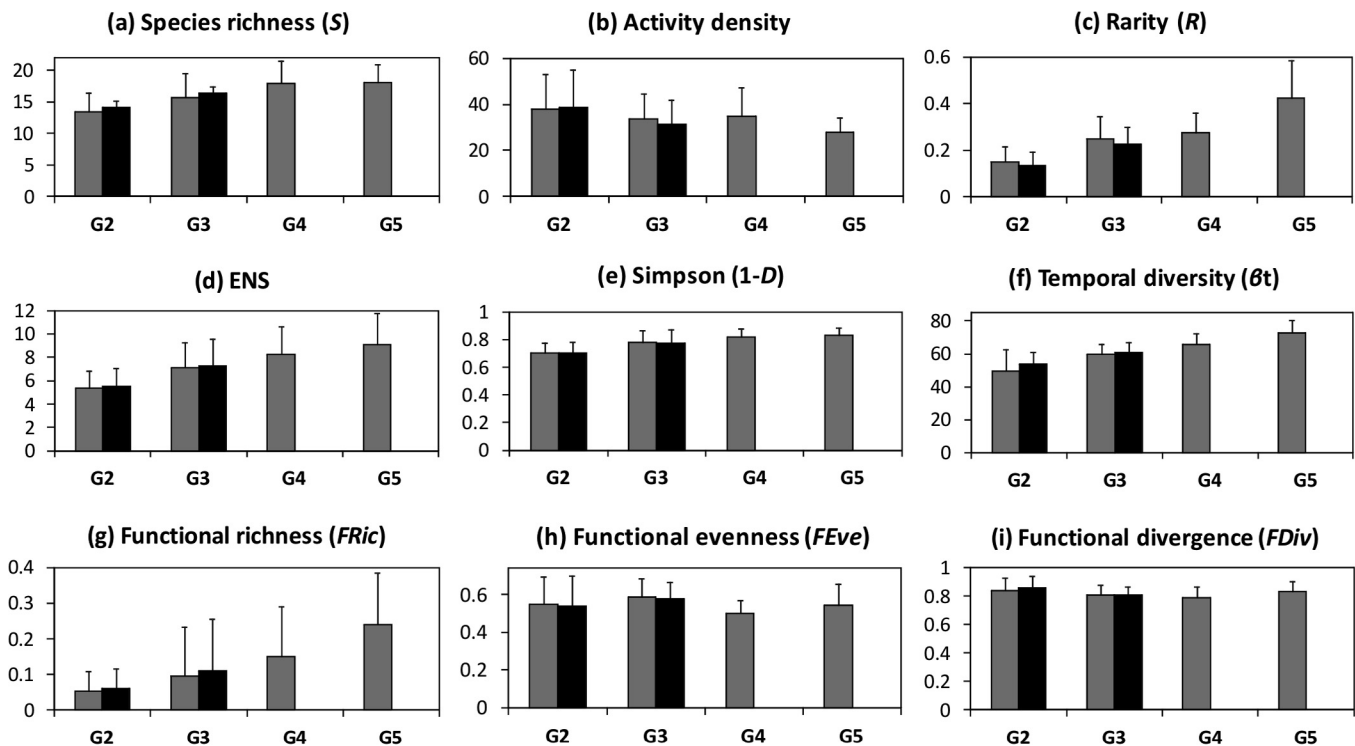


Fig. 4. Average \pm S.D. of (a) species richness, (b) activity density (number of individuals per 100 trap-days), (c) rarity (R), (d) Effective Number of Species (ENS) (e) Simpson evenness $1-D$, (f) temporal diversity (βt), (g) functional richness ($FRic$), (h) functional evenness ($FEve$), (i) functional divergence ($FDiv$) of gnaphosid communities under increasing levels of grazing (G2–G5). Black bars represent G2 and G3 sites excluding ALT4 sites (there were no G4 and G5 sites at ALT4).

graze even more extensively. Changes in vegetation structure and consequently microclimate (especially temperature and humidity) as well as prey availability affect spiders, while trampling causes a decline particularly in gnaphosid richness (Bell et al., 2001). Gnaphosidae are known to prefer open habitats more than closed densely vegetated ones (Zografou et al., 2017) and therefore it is possible that for this special group of spiders a patchwork of short and tall vegetation generated by grazing will generally harbour the highest number of species. The fact that gnaphosid abundance declined and richness increased with increasing grazing intensity in our study implies that more opportunistic ground spider species withstand high levels of this kind of disturbance but are present in smaller numbers.

The aforementioned pattern was further confirmed by the significant increase of ‘true diversity’ (ENS), evenness ($1-D$), temporal turnover (βt), rarity (R) and functional richness ($FRic$) of gnaphosid assemblages with increasing grazing intensity (Fig. 4d–g), refuting all parts of our third hypothesis and opposing the *a priori* expectation of low diversity under high levels of disturbance. Indeed, diversity indices of spider assemblages are reported as lowest at intensively grazed areas (Bromham et al., 1999; Warui et al., 2005) or unaffected by grazing (Churchill, 1998; Downie et al., 1999). The relative abundance patterns from G2 to G5 sampling sites highlight that the diversity patterns along differing grazing regimes mainly depend on the tolerance of dominant species (negatively affected by grazing) to disturbance. The activity density of the most abundant gnaphosid species on Crete, *P. lentiginosa*, which is known to avoid disturbance (Kaltsas et al., 2014), was significantly lower at overgrazed sites, where the available niche space was occupied by several synanthropic and indigenous species. The same was found by Kaltsas et al. (2013) for two of the commonest ground beetle species on Crete, *Carabus banoni* and *Cymindis lineata*, which were significantly more abundant in G2 than G5 sites. The activity density of synanthropic gnaphosid species was significantly higher in overgrazed sites when compared to the other grazing levels, even though they did not reach dominance in overgrazed sites. The opportunistic species hypothesis (OSH) (Gray, 1989) is therefore not

supported *per se*, i.e. by visualizing patterns of retrogression to dominance by opportunistic species, but on the other hand, an obvious transformation of the community pattern is observed, favouring synanthropic and otherwise rare indigenous species. OSH has been verified for epigeal spiders along urban-rural gradients (Horváth et al., 2012; Kaltsas et al., 2014), but not along differing grazing levels. Synanthropic species are mainly transported by humans and therefore they are expected to be comparatively more abundant in city centers than in remote natural habitats. Thus, the increased evenness in overgrazed areas of Crete may be ascribed to the high number of species tolerant to overgrazing induced conditions and also to the nature and intensity of disturbance (Kaltsas et al., 2013, 2014; Zakkak et al., 2014).

Despite the fact that functional and species evenness are usually closely related (Villéger et al., 2008), the two were weakly correlated in our study and $FEve$ and $FDiv$ did not differ among altitudinal classes, habitat types and grazing levels (Table 5), implying a similar distribution of species in functional trait spaces with respect to all environmental factors examined. However, the only functional diversity metric that does not incorporate abundance, ($FRic$) showed a distinct pattern (Fig. 4g), identical to that of effective number of species, evenness, temporal diversity and rarity, and contrary to the findings of Leroy et al. (2014) (decrease of $FDiv$ and rarity). Hence, the volume of functional space filled by gnaphosid assemblages in our study increased significantly with increasing grazing intensity, showing that the species that colonize highly disturbed sites are not ‘widespread but specialists’, as was found by Leroy et al. (2014). These species are functionally more diverse and rarer than those that form the assemblages in relatively undisturbed sites. This finding opposes the general predictions of Mouillot et al. (2013) regarding functional diversity metrics along disturbance gradients, as species extinction simply did not occur at overgrazed sites, leading to higher trait variability at overgrazed areas. Possibly the steep decrease in the abundance of the most dominant species (e.g. *P. lentiginosa*) in overgrazed sites evokes competitive release and allows the presence of species otherwise excluded by competition. Hence, even though diversity does not decrease under high

levels of grazing, this pattern is partially in accordance with the intermediate disturbance hypothesis (IDH), in terms of a trade-off between the species' competitive ability and their ability to tolerate disturbance, which prevents dominant species from excluding other species (Sasaki et al., 2009). Besides, the high values of temporal beta diversity for overgrazed sites reflect the high level of change in assemblage composition from each sampling period to the next. The fact that the highest values of temporal species turnover were calculated for overgrazed and intensively grazed sites in different habitat types and altitudinal classes of west, south, central and eastern Crete, rules out the concept of good adaptation to temporally changing ecological conditions, i.e. drastic seasonality (Zamora et al., 2007), and supports the pattern of mutual avoidance of species due to resource limitation (Romanuk and Kolasa, 2001; Kaltsas et al., 2012a, 2013). Since most of these species share the same hunting patterns and more or less the same prey repertoire (Chatzaki, 2003), their slightly differing peaks of annual activity during the favourable period of the year are attributed to avoidance of interspecific competition (Uetz, 1977). Temporal beta diversity was significantly lower at sites in subalpine shrublands where few species were active and co-occurrent during most of the year. This is due to the fact that in those sites the favourable activity period for Gnaphosidae is shorter within a year and hence the temporal turnover of ground spider species is generally low.

To summarize, assemblages in overgrazed sites on Crete are characterized by the presence of many scarce populations of mostly rare, functionally diverse gnaphosid species which partly replace Cretan endemic species and other common species on the island. Under released pressure conditions by high competitors, few or several individuals of species tolerant to high levels of disturbance enter these assemblages and occupy the few available microhabitats. Grazing is one of the oldest human activities on Crete and an essential part of the ecosystems of the island (Vogiatzakis and Rackham, 2008). It seems that it has been a continuous trigger for ecological plasticity of indigenous gnaphosids, which coexist with synanthropic species. The small populations of these species avoid competition and withstand low prey availability by shortening their phenologies through low temporal co-occurrence. Signifying a successful long term response of this taxon to the occurring habitat changes, this pattern induces high taxonomic evenness and significantly higher trait variability of co-occurrent species.

4.3. Implications for conservation

Grazing management in Crete is a very important conservation issue, especially since degradation in overgrazed areas is particularly aggravated, due to the extended drought in arid areas, leading to habitat loss. Priority should be given to the conservation of natural populations of indigenous, endemic and endangered species. In our study, overgrazed sites are pastures, degraded areas where indigenous phryganic shrubs are very sparse or absent. The overgrazed coastal and inland shrublands which include habitats of high conservation importance (Dimopoulos et al., 2006) are also of high management priority because in these formations introduced gnaphosid species replace endemic species, while these pastures support generally infrequent taxa of high conservation priority for Greece. The probable overall low size of these spiders' populations (as reflected by the here recorded low activity density) raises concern for management of these habitats in order to sustain if not to improve their capacity for survival of the species.

In situations where degradation is reversible, the application of appropriate grazing management is a viable solution towards restoration (Papanastasis, 2009). The declared numbers of livestock in Crete are unreliable and grazing has increased immensely since the 1980s mainly due to subsidies which were purchased by stock breeders and the non-implementation of environmental laws in Greece during the past decades. The first step is the application of management planning

according to the conservation priority of the habitat types of various shrublands in Crete (Dimopoulos et al., 2006; Kaltsas et al., 2013). To achieve ecosystem maintenance or even upgrade to higher vegetal formations, the moderation and the spatiotemporal discontinuity of grazing is essential. The arborescent and matorral species are well adapted to grazing pressure and its impacts on soil structure (e.g. rapid moisture loss) (De Bello et al., 2005) and have high recovery rate when grazing pressure is reduced (Tsiourlis et al., 2001). Thus, a flexible strategy implementing rotational grazing management including rested patches would help maintain spatial variability, varied vegetation structure and hence the microhabitats of epigeic indigenous and especially endemic and endangered invertebrate fauna.

5. Conclusion

Our study highlights ground spiders as significant indicators of grazing pressure on species and assemblage level on Crete. Gnaphosidae are a spider group which can tolerate human induced disturbances, including effects of long-term grazing, as depicted from Cretan ecosystems. Therefore, increasing grazing intensity caused a significant increase of average species richness, evenness, taxonomic, temporal and functional diversity, contradicting many relevant previous studies. Nevertheless, these differences may be due to the different habitat types, livestock species, grazing intensity, the sampling method used and the taxonomic level of focus chosen in each study. Taking these reservations into account, the need for a taxonomic focus within animal groups is imperative to avoid generalizations and unveil patterns on species and assemblage level. Gnaphosid spiders serve as the ideal evidence that significant patterns may arise even within the theoretically narrow functional space of co-familial species.

Acknowledgements

We would like to thank the director of the Natural History Museum of Crete Prof. Moysis Mylonas for entrusting us with the majority of the specimens studied in this paper and the multiple collectors/technicians who contributed to the sampling, sorting and storing of this material. We are also grateful to Manolis Nikolakakis for designing the map in Fig. 1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.04.024>.

References

- Allen, H.D., 2003. Response of past and present Mediterranean ecosystems to environmental change. *Prog. Phys. Geogr.* 27, 359–377.
- Baudry, J., Asselin, A., 1991. Effects of low grazing pressure on some ecological patterns in Normandy, France. *Opt. Méditerran. Sér. A* 15, 103–109.
- Bell, J.R., Wheeler, C.P., Cullen, W.R., 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. *J. Zool.* 255, 377–387.
- Blaum, N., Seymour, C., Rossmanith, E., Schwager, M., Jeltsch, F., 2009. Changes in arthropod diversity along a land use driven gradient of shrub cover in savanna rangelands: identification of suitable indicators. *Biodivers. Conserv.* 18 (5), 1187–1199.
- Blondel, J., 2006. The 'design' of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. *Hum. Ecol.* 34, 713–729.
- Bonte, D., Maelfait, J.-P., Hoffmann, M., 2000. The impact of grazing on spider communities in a mesophytic calcareous dune grassland. *J. Coast. Conserv.* 6, 135–144.
- Bromham, L., Cardillo, M., Bennett, A.F., Elgar, M.A., 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. *Aust. J. Ecol.* 24, 199–207.
- Chatzaki M., 2003. Ground spiders of Crete (Araneae, Gnaphosidae): Taxonomy, Ecology and Biogeography (Ph.D. thesis [in Greek]), University of Crete, 452.
- Chatzaki, M., Kaltsas, D., 2018. Fascinated by the unknown: research progress in the study of the spiders of Greece during the last twenty years. In: Sfenthourakis, S., Pafilis, P., Parmakelis, A., Poulakakis, N., Triantis, K.A. (Eds.), *Biogeography and Biodiversity of the Aegean. In Honour of Prof. Moysis Mylonas*. Broken Hill Publishers Ltd, Nicosia, Cyprus, pp. 107–122.
- Chatzaki, M., Trichas, A., Markakis, G., Mylonas, M., 1998. Seasonal Activity of the

- Ground Spider Fauna in a Mediterranean ecosystem (Mt. Yountas, Crete, Greece). In: Selden, P.A. (Ed.), *Proceedings of 17th Colloquium of Arachnology*. British Arachnological Society, pp. 235–244.
- Chatzaki, M., Lymberakis, P., Markakis, G., Mylonas, M., 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. *J. Biogeogr.* 32, 813–831.
- Chatzaki, M., Pitta, E., Poursanidis, D., Komnenov, M., Gloor, D., Nikolakakis, M., Nentwig, W., 2015. SPIDonet.gr – Spiders of Greece, Version 1.0. www.araneae.nmbe.ch/spidonet (accessed 07 January 2019).
- Churchill, T.B., 1998. Spiders as ecological indicators in the Australian tropics: family distribution patterns along rainfall and grazing gradients. In: Selden, P.A. (Ed.), *Proceedings of the 17th European Colloquium of Arachnology*, Edinburgh 1997. Burnham Beeches, Bucks, British Arachnological Society, pp. 325–330.
- Churchill, T.B., Ludwig, J.A., 2004. Changes in spider assemblages along grassland and savanna grazing gradients in Northern Australia. *Rangeland J.* 26 (1), 3–16.
- Colwell, R.K., 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9.1.0. – User's Guide and application. <http://viceroy.eeb.uconn.edu/estimates> (accessed 07 January 2019).
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. B* 345, 101–118.
- Cornwell, W.K., Schilck, D.W., Ackerly, D.D., 2006. A trait-based test for habitat filtering: convex hull volume. *Ecology* 87, 1465–1471.
- De Bello, F., Lepš, J., Sebastia, M.T., 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *J. Appl. Ecol.* 42, 824–833.
- De Keer, R., Alderweireldt, M., Declercq, K., Segers, H., Desender, K., Maelfait, J.-P., 1989. Horizontal distribution of the spider fauna of intensively grazed pastures under the influence of diurnal activity and grass height. *J. Appl. Ecol.* 107, 455–473.
- Dennis, P., Young, M.R., Bentley, C., 2001. The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. *Agric. Ecosyst. Environ.* 86, 39–57.
- Dennis, P., Skartveit, J., Kunaver, A., McCracken, D.I., 2015. The response of spider (Araneae) assemblages to structural heterogeneity and prey abundance in submontane vegetation modified by conservation grazing. *Global Ecol. Conserv.* 3, 715–728.
- Di Castri, F., 1981. Mediterranean-type shrublands of the world. In: di Castri, F., Goodall, D.W., Specht, R.L. (Eds.), *Mediterranean-type Shrublands of the World Ecosystems of the World 11: Mediterranean-type Shrublands*. Elsevier, Amsterdam, pp. 1–52.
- Dimopoulos, P., Bergmeier, E., Fischer, P., 2006. Natura 2000 habitat types of Greece evaluated in the light of distribution, threat and responsibility. *Biol. Environ.* 106B (3), 175–187.
- Downie, I.S., Wilson, W.L., Abernethy, V.J., McCracken, D.I., Foster, G.N., Ribera, I., Murphy, K.J., Waterhouse, A., 1999. The impact of different agricultural land-uses on epigeal spider diversity in Scotland. *J. Insect Conserv.* 3, 273–286.
- Dufrène, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Ehrlich, P., Ehrlich, A., 1981. *Extinction: The Causes and Consequences of the Disappearance of Species*. Random House, New York.
- Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Trautman Richers, B., Lin, B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33.
- Ford, H., Garbutt, A., Jones, L., Jones, D.L., 2012. Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conserv. Divers.* 6 (2), 189–200.
- Fuller, L., Newman, M., Irwin, S., Kelly, T., O'Halloran, J., 2014. Ground-dwelling spider diversity in rare European oak and yew woodlands and the impact of grazing. *Biodivers. Conserv.* 23, 1911–1929.
- Gerlach, J., Samways, M., Pryke, J., 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *J. Insect Conserv.* 17 (4), 831–850.
- Gibson, C.W.D., Hambler, C., Brown, V.K., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. *J. Appl. Ecol.* 29 (1), 132–142.
- Gray, J.S., 1989. Effects of environmental stress on species rich assemblages. *Biol. J. Linn. Soc.* 37, 19–32.
- Hadjigeorgiou, I., Vallerand, F., Tsimopoulos, K., Zervas, G., 2002. The socio-economics of sheep and goat farming in Greece and the implications for future rural development. *Opt. Méditerran. Sér. B* 39, 83–93.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4 (1), 9. http://palaeoelectronica.org/2001_1/past/issue1_01.htm (accessed 07 January 2019).
- Harris, R., York, A., Beattie, A.J., 2003. Impacts of grazing and burning on spider assemblages in dry eucalypt forests of north-eastern New South Wales, Australia. *Aust. Ecol.* 28, 526–538.
- Hill, J., Hostert, P., Tsiourlis, G., Kasapidis, P., Udelhoven, T., Diemer, C., 1998. Monitoring 20 years of increased grazing impact on the Greek island of Crete with earth observation satellites. *J. Arid Environ.* 39 (2), 165–178.
- Horvat, I., Glavač, V., Ellenberg, H., 1974. *Vegetation Südosteuropas*. Geobotanica selecta 4. Gustav Fischer Verlag, Stuttgart.
- Horváth, R., Magura, T., Tóthmérész, B., 2012. Ignoring ecological demands masks the real effect of urbanization: a case study of ground-dwelling spiders along a rural-urban gradient in a lowland forest in Hungary. *Ecol. Res.* 27, 1069–1077.
- Jost, L., 2006. Entropy and diversity. *Oikos* 113 (2), 363–375.
- Kaltsas, D., Trichas, A., Mylonas, M., 2012a. Temporal organization patterns of epigeal beetle communities (Coleoptera: Carabidae, Tenebrionidae) in different successional stages of eastern Mediterranean maquis. *J. Nat. Hist.* 46 (7–8), 495–515.
- Kaltsas, D., Panayiotou, E., Trichas, A., Chatzaki, M., Mylonas, M., 2012b. Co-occurrence patterns and shaping processes of assembly in beetle and spider communities in eastern Mediterranean maquis formations. *J. Biol. Res. (Thessaloniki)* 18, 187–197.
- Kaltsas, D., Trichas, A., Kouglioumoutzis, K., Chatzaki, M., 2013. Ground beetles respond to grazing at assemblage level, rather than species-specifically: the case of Cretan shrublands. *J. Insect Conserv.* 17, 681–697.
- Kaltsas, D., Panayiotou, E., Chatzaki, M., Mylonas, M., 2014. Ground spider assemblages (Araneae: Gnaphosidae) along an urban-rural gradient in the city of Heraklion, Greece. *Eur. J. Entomol.* 111 (1), 59–67.
- King, K.L., Hutchinson, K.J., 2007. Pasture and grazing land: assessment of sustainability using invertebrate bioindicators. *Aust. J. Exp. Agric.* 47, 392–403.
- Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conserv. Biol.* 7, 796–805.
- Labiberté, E., Legendre, P., Shipley, B., 2014. FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12.
- Legakis, A., Maragou, P., 2009. *The Red Data Book of the Threatened Animals of Greece*. Hellenic Zoological Society, Athens [in Greek].
- Leroy, B., Le Viol, I., Pétillon, J., 2014. Complementarity of rarity, specialisation and functional diversity metrics to assess community responses to environmental changes, using an example of spider communities in salt marshes. *Ecol. Indic.* 46, 351–357.
- Lubin, Y., Angel, N., Assaf, N., 2011. Ground spider communities in experimentally disturbed Mediterranean woodland habitats. *Arachnol. Mitt.* 40, 85–93.
- Lyons, A., Ashton, P.A., Powell, I., Oxbrough, A., 2018. Epigeal spider assemblage responses to vegetation structure under contrasting grazing management in upland calcareous grasslands. *Insect Conserv. Divers.* 11 (4), 383–395.
- Lyrantzis, G.A., 1996. Human impact trend in Crete: the case of Psilorites Mountain. *Environ. Conserv.* 23 (2), 140–148.
- McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.0. MjM Software, Gleneden Beach, Oregon, USA.
- McCune, B., Grace, J.B., Urban, D.L., 2002. *Analysis of Ecological Communities*. MjM Software Design.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28 (3), 167–177.
- Naem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. *Science* 336, 1401–1406.
- Niemelä, J., Langor, D., Spence, J.R., 1993. Effects of clear-cut harvesting on boreal ground beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conserv. Biol.* 7 (3), 551–561.
- Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Response of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77, 290–310.
- Paschetta, M., La Morgia, V., Masante, D., Negro, M., Rolando, A., Isaia, M., 2013. Grazing history influences biodiversity: a case study on ground-dwelling arachnids (Arachnida: Araneae, Opiliones) in the Natural Park of Alpi Marittime (NW Italy). *J. Insect Conserv.* 17, 339–356.
- Papanastasis, P., 2009. Restoration of degraded grazing lands through grazing management: can it work? *Restoration Ecol.* 17 (4), 441–445.
- Papanastasis, B.P., Noitsakis, B.I., 1992. *Rangeland ecology*. Thessaloniki, Greece [in Greek].
- Perevolotsky, A., Seligman, N.G., 1998. Role of grazing in Mediterranean rangeland ecosystems. *Bioscience* 48, 1007–1017.
- Pétillon, J., Georges, A., Canard, A., Ysnel, F., 2007. Impact of cutting and sheep grazing on ground-active spiders and carabids in intertidal salt marshes (Western France). *Anim. Biodivers. Conserv.* 30 (2), 201–209.
- Prieto-Benítez, S., Méndez, M., 2011. Effects of land management on the abundance and richness of spiders (Araneae): a meta-analysis. *Biol. Conserv.* 144, 683–691.
- Quézel, P., Barbero, M., 1982. Definition and characterization of Mediterranean-type ecosystems. *Ecol. Mediterr.* 8, 15–29.
- R Development Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rackham, O., Moody, J., 1996. *The Making of the Cretan Landscape*. Manchester University Press, Manchester, NY.
- Romanuk, T.N., Kolasa, J., 2001. Simplifying the complexity of temporal diversity dynamics: a differentiation approach. *Ecoscience* 8, 259–263.
- Sasaki, T., Okubo, S., Okayasu, T., Jamsran, U., Ohkuro, T., Takeuchi, T., 2009. Management applicability of the intermediate disturbance hypothesis across Mongolian rangeland ecosystems. *Ecol. Appl.* 19, 423–432.
- Simaiki, S., Minelli, A., Mylonas, M., 2005. The centipede fauna of the Aegean archipelago (Greece, eastern Mediterranean). *Isr. J. Zool.* 51, 241–307.
- Szinétár, C., Samu, F., 2012. Intensive grazing opens spider assemblage to invasion by disturbance-tolerant species. *J. Arachnol.* 40 (1), 59–70.
- Tsiourlis, G.M., Kasapidis, P., Konstantinidis, P., 2001. Effects of grazing on the structure and dynamics of Mediterranean ecosystems in Central Crete, Greece. *Proceedings International Conference Forest Research: a challenge for an integrated European approach*, Thessaloniki, Greece, 27 August–1 September 2001, Volume II. NAGEF-Forest Research Institute.
- Tzanopoulos, J., Mitchell, J., Pantis, J.D., 2007. Vegetation dynamics in abandoned crop fields on a Mediterranean island: Development of succession model and estimation of disturbance thresholds. *Agric. Ecosyst. Environ.* 120, 370–376.
- Uetz, G.W., 1977. Coexistence in a guild of wandering spiders. *J. Anim. Ecol.* 46, 531–541.
- van Klink, R., Ruifrok, J.L., Smit, C., 2016. Rewilding with large herbivores: Direct effects and edge effects of grazing refuges on plant and invertebrate communities. *Agric. Ecosyst. Environ.* 234, 81–97.
- Verdú, J.R., Crespo, M.B., Galante, E., 2000. Conservation strategy of a nature reserve in Mediterranean ecosystems: the effects of protection from grazing on biodiversity.

- Biodivers. Conserv. 9, 1707–1721.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
- Vogiatzakis, I.N., Rackham, O., 2008. Chapter 11: Crete. In: Vogiatzakis, I.N., Pungetti, G., Mannion, A. (Eds.), *Mediterranean island landscapes: Natural and cultural approaches*. Landscape series, vol. 9. Springer, pp. 245–270.
- Waloff, N., 1980. Studoes on grassland leafhoppers (Auchenorrhyncha, Homoptera) and their natural enemies. *Adv. Ecol. Res.* 11, 82–215.
- Warui, C.M., Villet, M.R., Young, T.P., Jocque, R., 2005. Influence of grazing by large mammals on the spider community of a Kenyan savanna biome. *J. Arachnol.* 33, 269–279.
- World Spider Catalog, 2018. World Spider Catalog. Natural History Museum Bern. <http://wsc.nmbe.ch>, version 19.5 (accessed 07 January 2019). doi: 10.24436/2.
- Zakkak, S., Chatzaki, M., Karamalis, N., Kati, V., 2014. Spiders in the context of agricultural land abandonment in Greek mountains: species responses, community structure and the need to preserve traditional agricultural landscapes. *J. Insect Conserv.* 18 (4), 599–611.
- Zamora, J., Verdú, J.R., Galante, E., 2007. Species richness in Mediterranean agroecosystems: spatial and temporal analysis for biodiversity conservation. *Biol. Conserv.* 134, 113–121.
- Zografou, K., Adamidis, G.C., Komnenov, M., Kati, V., Sotirakopoulos, P., Pitta, E., Chatzaki, M., 2017. Intra-seasonal activity of spiders and Orthoptera along a canopy cover gradient. *J. Insect Conserv.* 21 (3), 1–13.