

POST-FIRE FUEL AND VEGETATION DYNAMICS IN AN UNGRAZED PHRYGANIC COMMUNITY OF CRETE, GREECE

ELHAG, M.^{1*} – YILMAZ, N.² – DUMITRACHE, A.³

¹*Department of Hydrology and Water Resources Management, Faculty of Meteorology,
Environment & Arid Land Agriculture, King Abdulaziz University
Jeddah 21589, Saudi Arabia*

²*Department of Freshwater Resources and Management, Faculty of Aquatic Sciences, Istanbul
University, Ordu St. No. 200, Laleli, Istanbul, Turkey*

³*Institute of Biology Bucharest, Romanian Academy, Department of Ecology, Taxonomy and
Nature Conservation, Splaiul Independentei No. 296, Bucharest 060031, Romania*

**Corresponding author
e-mail: melhag@kau.edu.sa*

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Abstract. Phrygana is a widespread vegetat type in the eastern Mediterranean, mainly represented by *Sarcopoteriwn spinosum* dominated formations in the Aegean islands and Crete. The effects of overgrazing and frequent burnings on phrygana are relatively known by scientists, but limited attention has been paid to the functioning of these communities when grazing and fires are suppressed. The aim of this study is to investigate post-fire vegetation and fuel dynamics in an ungrazed *S. spinosium* dominated phrygana in northwestern Crete. Fuel was first analyzed according to shrub, herb, litter, and total load; then live and dead materials; and finally, 0-0.5 cm and 0.6-2.5 cm of leaf diameter classes. Vegetation was analyzed based on cover and life form composition and dynamics. Also, species richness, diversity, and dynamics were investigated. One-way ANOVA was used to test for fuel and vegetation differences among sites, and Shannon-Wiener and Equitability indices were used to assess both diversity and evenness. Results showed a rapid reestablishment of both the vegetation (cover, life form, species richness and diversity) and fuel, as early as the 3rd and the 6th post-fire year, respectively. Fuel and vegetation were tremendously dominated by unpalatable and highly flammable dwarf shrubs, which smothered herbaceous plants. Species diversity was relatively low, indicating that few species crushingly structured the community by their high cover, while the remaining species were poorly abundant. The implications of the results in the context of a rational management planning of phryganic ecosystems are discussed.

Keywords: *biomass, Phrygana, post-fire dynamics, species diversity, species richness, vegetation Cover*

Introduction

Many, if not all, ecosystems of the world are known to undergo cyclic processes of disturbances and recovery, occurring at specific spatiotemporal scales. These natural phenomena allow ecosystems to maintain their ecological processes as well as their biological and ecological diversity in space and time (Naveh, 1994).

At least since the Jurassic geological time, fires had always been a natural selective force which affected plant community structure, productivity, and species composition (Le Houerou, 1974; Trabaud, 1994, 2000). In addition, fires have been associated with species diversity maintenance (Christensen, 1985), have contributed to stands rejuvenation (Trabaud, 2000), and have allowed species coexistence in space and time, by interrupting competitive advantage of dominant species (Malanson, 1987).

Mediterranean forests and shrublands exemplify the abovementioned ecological systems that cope with natural disturbances such as natural fires' and grazing by wildlife.

As far as post-fire plant demography in phrygana is concerned, documented a great deal of dwarf shrubs' seed germination and seedling recruitment during the first post-fire year, contrasting with the unburned phrygana (Arianoutsou, 1998). By far, the dominant seedlings were made up of *Cistus* spp. and *Sarcopoterium spinosum* (with numbers multiplied by 10 and 20 times). On the contrary, a low seed germination level portrayed dwarf shrub in the 2nd post-fire year; 10 seeds per m² for *Cistus* spp. and 3 seeds per m² for *S. spinosum* were counted in winter. A similar demographic trend has also been reported for other phryganic communities by Naveh (1974), Papanastasis (1977), and Arianoutsou (1998), that is, a decrease in a number of dwarf shrubs' seedlings during the first post-fire year, and no conspicuous seed germination during the 2nd post-fire year. It is worthwhile referring that two main hypotheses have been suggested to explain the decrease in seedling density. The negative effects of the hot and dry Mediterranean summer on dwarf shrub seedlings' survival (Ferran et al., 1998) or the strong inhibiting competition exerted by the massive herbaceous plants on the young dwarf shrubs' recruits (Henkin et al., 1999; Seligman and Henkin, 2000).

Regarding to the post-fire fuel/biomass dynamics, there is insufficient research has been devoted to ecosystem structure and post-fire fuel dynamics in phryganic ecosystems. In Greece, the little literature available on the subject focused mainly on aboveground net primary production, whereas fuel and fire hazard-oriented studies are almost lacking. It is worthwhile mentioning that Christensen (1985) also highlighted the substantial contribution of herbaceous plants to shrubland production in immediate post-fire years.

To our knowledge, Papanastasis (1980) have provided the scanty, but useful, information available on fuel characteristics in Greek phrygana in relation to fire hazard. Thereby, the latter author mentioned that phryganic ecosystem are inclined to accumulate dead material as they age; thus, becoming decadent if unburned. This characteristic coupled with small sized material featuring phryganic dwarf shrubs contribute to render the older communities highly flammable (Papanastasis, 1977). However, as reported by Papanastasis (1980) in an experimental study, *Sarcopoterium spinosum* plants did not burn easily unless enough dead fuel had existed on them. This latter fuel required, at least, three post-fire years to be accumulated. Additionally, it has been indicated that herbaceous plants occurring in phryganic formations are also fire-adapted. Indeed, some species, such as *Andropogon hirtus*, a perennial grass that retains its old growth, contribute to the flammability of the phrygana (Papanastasis, 1977). Finally, fuel distribution has been documented to be uniform only on old and thick phrygana with no or few herbaceous plants. Most often, fuel is discontinuously distributed in grazed communities, made up of dwarf shrubs and herbaceous plants fairly intermingled (Papanastasis, 1977, 2000).

Studies have reported that both high ecosystem diversity and landscape maintenance in the Mediterranean have been promoted and ensured by the cyclic disturbances properly induced by humans and their livestock (Naveh, 1994; Naveh and Whittaker, 1980, 2007). However, improper land use such as wildfires and overgrazing for decades has significantly altered the ecosystems, and more particularly rangelands, such as phrygana in the eastern Mediterranean. Therefore, the objectives of the current research are to investigate post-fire fuel and vegetation dynamics in an ungrazed *Sarcopoterium*

spinosum dominated phryganic community in northwestern Crete (Greece) for a relatively short period; that is, between 3 and 12 years.

Materials and Method

Study area general description

The study area is represented by the hills of Malaxa situated in northwestern Crete (Figure 1). This part of the island is administratively managed by the Prefecture of Chania, and more specifically by the municipality of Souda. The climate of Chania is typically the Mediterranean, characterized by a long dry summer season with a monotone wind regime, and precipitations ranging from September to May (Elhag and Bahrawi, 2016). The recent climatic data of Chania, for the last 20-year-period, indicated an annual precipitation averaging 690.4 mm. The Bagnouls-Gausson ombrothermic diagram, drawn from the abovementioned data displays a longer dry summer period than mentioned by Elhag and Bahrawi (2016), beginning in April and ending in mid-September. The rainy period, ranging from October to March is characterized by an average precipitation of 615.65 mm, and the xerothermic period, extending from April to September, reaches 74.75 mm only. It is worth noting that January and February are the coldest months, with an average temperature of 10.6 °C, and July the hottest month with an average of 24.7 °C. Based on Emberger's pluviothermic quotient value (Q=86) calculated for Chania, Elhag and Bahrawi (2018) classified this region in the subhumid Mediterranean bioclimate. The differences among the designated study sites were evaluated based on its soil chemical properties (Table 1).



Figure 1. Study area vegetation cover located at Malaxa, Crete

Table 1. Chemical properties of soil samples taken from the four sites

	Soil Chemical Properties							
	pH	Org. Matt.*	N*	P**	Mg**	Ca**	K**	Na**
Site 1 [3 years]	6.51	5.12	0.35	0.81	2.19	21.25	0.25	0.22
Site 2 [6 years]	6.36	5.87	0.38	0.82	2.65	19.85	0.27	0.21
Site 3 [9 years]	6.21	6.61	0.41	0.82	3.11	17.25	0.31	0.22
Site 4 [12 years]	6.16	6.96	0.44	0.81	3.64	15.74	0.33	0.23

* (%), ** (mg/100 g soil)

Sampling techniques and procedures

Fuel sampling and procedural steps

Sampling location was randomly selected in the central part of a physiognomically homogeneous vegetation, and line-transects were run in four directions from a central point. Each line-transect was 15 m long and one plot was taken at the end. The total number of plots per site was four. In each 1 m²-plot, all the aboveground biomass was clipped and put in a plastic bag. As regards the laboratory work, the first step consisted in fuel separation to shrub, herb, and litter. Shrub was then divided to live and dead parts. It is noteworthy that live material included green leaves and fresh twigs, whereas dead material all the parts devoid of living tissues. Afterward, live and dead materials were separated into two leaf diameter classes: 0-0.5 cm and 0.6-2.5 cm. Finally, the fuel was oven dried at a temperature of 105° C for 24 hours, then weighted with a digital balance according to the categories.

Vegetation sampling and procedural steps

Vegetation sampling was carried out in the central part of a physiognomically homogeneous vegetation to ensure samples' representativeness and to avoid any edge effects. In each sampling location, four line-transects were run from a central point. Following the scheme used in fuel sampling, but transect length was 20 m. Cover values of plants, litter, and bare ground were then recorded using Line Transect and Point Intercept methods combined (Bonham, 1995); a 20 m measuring tape was stretched between two stakes along the line-transect, and a pin was dropped perpendicularly to the tape each 20 cm interval. Observations were recorded by reading the hits. The laboratory work was conducted in a herbarium: plant specimens were identified with the help of a stereoscope and the descriptive keys of Flora Europaea referential volumes (Tutin et al., 1980).

Analytical procedures and statistical treatments

Fuel analysis

Fuel was analyzed according to the several categorizations based on the fuel separation to shrub, herb, and litter, fuel separation to live, dead materials, and fuel separation to diameter classes. Post-fire changes in fuel composition and dynamics were investigated at the abovementioned three category levels. Analysis of variance (one-way ANOVA) was used to test for fuel load differences among sites, and Duncan multiple range tests for mean pair's comparisons.

Vegetation composition

Vegetation composition was analyzed based on shrub and herbaceous covers. In each site, both percent cover and percent cover composition were calculated according to the following two formulae of Bonham (1995):

1. Percent cover = (number of point intercepts / total points) x 100.
2. Percent cover composition = (number of point intercepts / total point intercepts of vegetation) x 100.

Floristic composition

Floristic composition was analyzed based on life form richness. Following are the different life form groups (Kent, 2011):

- Phanerophytes: species with perennating buds emerging from aerial parts of the plant.
- Chamaephytes: species with perennating buds borne on aerial parts close to the ground (below 2 m).
- Geophytes: species with buds or shoot apices, which survive the unfavorable period below ground.
- Hemicryptophytes: all aboveground parts of the plant die back in unfavorable conditions, and buds are borne at ground level.
- Therophytes: plants that survive the unfavorable period as seeds. Species are annuals and complete their life cycle from seed to seed in the favorable summer months.

Species richness

Post-fire species richness dynamics was described using the following two ecological parameters (Blondel and Aronson, 1995; Magurran, 2013):

- A number of species per site, which combines the four lines-transects.
- Species richness per site, which is the sum of the total richness recorded in each line-transect of that site divided by the total number of line-transects ($n = 4$).

Species diversity

Post-fire species diversity dynamics was investigated using both heterogeneity and equitability (also referred as evenness) indices. Species diversity was calculated using the Shannon-Wiener heterogeneity index (H') which is based on the Information Theory (Naveh and Whittaker, 1980, 2007; Magurran, 2013). The formula is the following:

$$H' = -\sum_{i=1}^s (P_i)(\log_e P_i) \quad (\text{Eq.1})$$

where:

H' = the Information content of sample (nits/individual),

s = Number of species,

P_i = Abundance of the i^{th} species expressed as a proportion of total cover.

Equitability which refers to the pattern of distribution of individuals among species was calculated using the following index proposed by (Kent, 2011) based on Shannon-Wiener diversity index:

$$J = H' / H'_{\max} \quad (\text{Eq.2})$$

where:

J = the Equitability index,

H' = Shannon-Wiener diversity index,

$H'_{\max} = \log_e (s) =$ Maximum possible value of H' ,

s = Number of species.

The equitability index ranges from 0 to 1. It tends towards 0 when almost all abundances correspond to one species of the community, and towards 1 when each species is represented by the same abundance.

Species dynamics

Species dynamics was analyzed because of their cover changes throughout the different post-fire stages. The following community's characteristics were particularly brought out:

- The dominant species structuring the vegetation by its abundant cover.
- The diagnostic species of the community by their constant presence whatever fire interval considered.

Results

Post-fire fuel dynamics

In all sites, both shrub and litter accounted for about 97% of the total fuel composition. By far, shrub's contribution was the most important (about 80%). The herbaceous vegetation (about 3%) represented the remaining fuel. In addition, shrub, litter, and total fuel loads differed significantly ($p=0.003$, $p=0.034$, and $p=0.002$, respectively) among the sites, while herbaceous load did not ($p=0.508$) as it shown in *Table 2*.

Table 2. *Shrub, herb, litter, and total fuel loads (oven-dry weight) measured at four sites with different fire intervals (kg/ha)*

Site N [Fire interval]	Shrub			Herb	Litter	Total fuel
	Live	Dead	Total			
Site 1 [3 years]	3092.3 ^a	835.1 ^a	3927.4 ^a (84.0%)	209.2 (4.5%)	537.3 ^a (11.5%)	4673.9 ^a (100%)
Site 2 [6 years]	6097.5 ^c	6191.1 ^b	12288.6 ^b (83.7%)	459.7 (3.1%)	1928.7 ^{ab} (13.2%)	14677.0 ^b (100%)
Site 3 [9 years]	5044.3 ^{bc}	7284.9 ^b	12329.2 ^b (77.2%)	360.6 (2.2%)	3286.0 ^b (20.6%)	15975.8 ^b (100%)
Site 4 [12 years]	3986.4 ^{ab}	7380.6 ^b	11367.0 ^b (76.5%)	502.9 (3.4%)	2979.2 ^b (20.1%)	14849.1 ^b (100%)

Percentage of total fuel load between parentheses. Comparisons among sites performed by conducting one-way ANOVA and Duncan's Multiple Range Test, both at the $p=0.05$ level of significance. Values followed by the same letter are not statistically different

The results showed that shrub composed the bulk of the fuel between 3 and 12 years after fire. It is worth noting that a substantial amount of litter was accumulated as early as the 3rd post-fire year, whereas herbaceous biomass was lowly produced. Furthermore, a threefold amount of both shrubs and total fuel (about 12000 kg/ha and 15000 kg/ha, respectively) were noticed six years after fire, and a six-fold amount of litter (about 3000 kg/ha) nine years after fire, as compared to the amounts produced at the 3rd post-fire year. On the other hand, the statistical analyses suggested a stabilization of shrub, litter, and total fuel loads since the 6th post-fire year onwards.

Live and dead shrub fuel loads measured at the four sites with different fire intervals are presented in *Table 3*. The highest live material's contribution (about 80% of shrub

fuel composition) was noted in the 3rd post-fire year. On the contrary, the dead material was found highly accumulated (about 65% of shrub fuel composition) in the 12nd post-fire year. One must notice the similar proportions of both live and dead materials in the 6th post-fire year. Additionally, both live and dead fuel loads were found differing significantly ($p=0.038$ and $p=0.002$, respectively) among the sites and the following differences were highlighted in the multiple comparison tests (Elhag et al., 2017):

- Site 1 had significantly lower live fuel load (3092.3 kg/ha) than site 2, characterized by almost double biomass (6097.5 kg/ha). Otherwise, similar loads characterized the three oldest sites.
- Site 1 had significantly lower dead fuel load (835.1 kg/ha) than site 2, site 3, and site 4, characterized by similar high loads (about 7000 kg/ha).

Table 3. Live and dead shrub fuel loads (oven-dry weight) measured at the four sites with different fire intervals (kg/ha)

Site N [Fire interval]	Live fuel	Dead fuel	Total fuel
Site 1 [3 years]	3092.3 ^a (78.7%)	835.1 ^a (21.3%)	3927.4 ^a (100%)
Site 2 [6 years]	6097.5 ^c (49.6%)	6191.1 ^b (50.4%)	12288.6 ^b (100%)
Site 3 [9 years]	5044.3 ^b (40.9%)	7284.9 ^b (59.1%)	12329.2 ^b (100%)
Site 4 [12 years]	3986.4 ^{ab} (35.1%)	7380.6 ^b (64.9%)	11367.0 ^b (100%)

Percentage of live and dead fuel load between parentheses. Comparisons among sites performed by conducting one-way ANOVA and Duncan's Multiple Range Test, both at the $p=0.05$ level of significance. Values followed by the same letter are not statistically different

The results show that live material overwhelmingly dominated shrub fuel composition in the 3rd post-fire year, while the dead material was not substantially accumulated yet. On the other hand, a dead material composed the fuel bulk in the oldest post-fire stage (Elhag et al., 2017). Furthermore, the statistical analyses suggested that both live and dead fuel loads stabilized since the 6th post-fire year onwards, even though the following dynamic trends were noted:

- Live fuel load decrease since the 6th post-fire year onwards.
- Dead fuel load increase as early as the 3rd post-fire year onwards.

In all the sites, live fuel was almost entirely made up of material in the 0-0.5 cm diameter class. The latter size class material also dominated dead fuel composition (about 89%), while larger fuel in the 0.6-2.5 cm diameter class was poorly represented (about 11%). Additionally, live and dead fuel loads in the 0-0.5 cm diameter class differed significantly ($p=0.046$ and $p=0.001$, respectively) among the sites. On the contrary, dead fuel load in the 0.6-2.5 cm diameter class did not ($p=0.143$) as it shown in Table 4. Multiple comparison tests showed the following differences among the sites:

- Site 1 had significantly lower live fuel load in the 0-0.5 cm diameter class (3092.3 kg/ha) than site 2 characterized by a nearly twofold production (5832.5 kg/ha). Otherwise, similar loads characterized the three oldest sites.
- Site 1 had significantly lower dead fuel load in the 0-0.5 cm diameter class (796.9 kg/ha) than site 2, site 3, and site 4, characterized by similar high loads (about 6000 kg/ha).

Table 4. Live and dead shrub fuel loads (oven-dry weight) separated to diameter classes measured at the four sites with different fire intervals (kg/ha)

Site N [Fire interval]	Live fuel			Dead fuel		
	D[0-0.5]	D[0.6-2.5]	Total	D[0-0.5]	D[0.6-2.5]	Total
Site 1 [3 years]	3092.3 ^a (100%)	--	3092.3 ^a (100%)	796.9 ^a (95.4%)	38.2 (4.6%)	835.1 ^a (100%)
Site 2 [6 years]	5832.5 ^b (95.7%)	265.0 (4.3%)	6097.5 ^b (100%)	5840.2 ^b (94.3%)	350.9 (5.7%)	6191.1 ^b (100%)
Site 3 [9 years]	5044.3 ^b (100%)	--	5044.3 ^b (100%)	6356.6 ^b (87.3%)	928.3 (12.7%)	7284.9 ^b (100%)
Site 4 [12 years]	3986.4 ^b (100%)	--	3986.4 ^b (100%)	5742.2 ^b (77.8%)	1638.4 (22.2%)	7380.6 ^b (100%)

D: diameter class (cm)

Percentage of fuel load between parentheses. Comparisons among sites performed by conducting one-way ANOVA and Duncan's Multiple Range Test, both at the p=0.05 level of significance. Values followed by the same letter are not statistically different

Post-fire vegetation dynamics

In all sites, shrubs composed about 73% of the vegetation cover, whereas herbs and grasses contributed to about 27% only. With respect to the herbaceous component, it is worth noting that the most contributing species to total vegetation was the perennial grass *Brachypodium retusum* with an average cover amounting to about 3%. Additionally, both shrub and herbaceous covers did not differ significantly (p=0.269 and p=0.087, respectively) among the sites. The above results show that shrubs overwhelmingly structured the vegetation, whereas herbaceous contribution was not substantial. Overall vegetation cover stabilization was also detected as early as the 3rd post-fire year onwards (Elhag et al., 2017).

114 species belonging to 23 families were recorded in the community using the line transect and point intercept methods combined. The floristic composition based on life form richness in the four sites with different fire intervals is summarized in Table 5.

Table 5. Life form richness of the four sites with different fire intervals

Life forms	Site 1 [3 years]	Site 2 [6 years]	Site 3 [9 years]	Site 4 [12 years]
Phanerophytes	4 (9.8%)	3 (5.4%)	4 (6.6%)	4 (5.9%)
Chamaephytes	5 (12.2%)	7 (12.5%)	8 (13.1%)	7 (10.3%)
Geophytes	3 (7.3%)	2 (3.6%)	3 (4.9%)	2 (2.9%)
Hemicryptophytes	11 (26.8%)	19 (33.9%)	14 (22.9%)	17 (25.0%)
Therophytes	18 (43.9%)	25 (44.6%)	32 (52.5%)	38 (55.9%)
Total	41 (100%)	56 (100%)	61 (100%)	68 (100%)

Percentage of total life form groups for each site is given between parentheses

In all the sites, therophytes and hemicryptophytes were the most dominant life forms, both contributing to about 76% of the floristic composition. It is worthwhile mentioning that therophytes were, by far, the most represented life form (about 49%), followed by hemicryptophytes (about 27%). The remaining forms, in decreasing richness, were the chamaephytes (about 12%), phanerophytes (about 7%), and geophytes (about 5%).

The hemicryptophyte richness differed significantly ($p=0.002$) among the sites, whereas the other life forms did not ($p=0.208$, $p=0.144$, $p=0.554$, and $p=0.255$ for phanerophytes, chamaephytes, geophytes, and therophytes, respectively).

Multiple comparison tests showed the following differences among sites as regards hemicryptophyte richness:

- Site 2 had significantly higher mean richness than site 1, site 3, and site 4.
- Site 3 and site 4 were characterized by similar mean richness, lower than site 2.

In other respects, the statistical analyses revealed that species richness of phanerophytes, chamaephytes, geophytes, and therophytes did not differ significantly in all the studied post-fire stages, suggesting a stabilization process as early as the 3rd post-fire year onwards. On the other hand, it was noted a substantial increase of hemicryptophyte richness until the 6th post-fire year, and a decrease thereafter. The similar richness values obtained for the latter life form in the two oldest post-fire stages seemed to indicate a stabilization process since the 9th post-fire-year onwards. However, the study of a longer chronosequence is needed to confirm this latter suggestion (Elhag et al., 2017).

In *Table 6*, the number of species increased from site 1 ($S=44$) to site 4 ($S=74$). On the contrary, species richness was similar (s comprised between 16.75 and 22.75): no significant differences were detected among sites ($p=0.075$). Based on the latter ecological parameter which allows a subtle appreciation of the differences among sites, the results indicated that in all sites, an average of 21 species was collected in the covered transects. This average species number can be considered as representative of the community in each site (Blondel and Aronson, 1995; Magurran, 2013). Moreover, the species richness assigns to each species a weight that is proportional to its appearance probability along the sequence of transects; consequently, the less abundant species will be attributed a small weight (Blondel and Aronson, 1995; Magurran, 2013). On the other hand, it was noted that 70.4%, 70.2%, 85.1%, and 85.1% of the species occurring in site 1, site 2, site 3, and site 4, respectively, were recorded in one transect only and with a minimal cover value.

Table 6. A number of species and richness in the four sites with different fire intervals

Site N [Fire interval]	Site 1 [3 years]	Site 2 [6 years]	Site 3 [9 years]	Site 4 [12 years]
Number of species	44	57	67	74
Species richness	16.75 (± 1.25)	21.50 (± 0.29)	22.75 (± 1.25)	22.50 (± 2.72)

Standard error between parentheses

The values of heterogeneity index which were relatively low (less than 2.5) as compared to those usually obtained in more diversified communities (3.5). (Washington, 1984; Kent, 2011), suggested that in the four post-fire stages, the study phrygana was characterized by a relatively low diversity (*Table 7*). In other words, the environmental conditions prevailing in the community tended to be slightly unfavorable, allowing the settlement of a small number of species which were relatively abundant (Cowling et al., 1996). On the other hand, the values of mean equitability index (which did not exceed 0.7) suggested that in the covered transects, an appreciable number of species had a more or less similar importance, but few others were more abundant (Cowling et al., 1996).

The description of plant species dynamics suggests that three main characteristics portray the ungrazed phryganic community between 3 and 12 years after fire:

- One overwhelmingly dominant dwarf shrub species, *Sarcopoterium spinosum*, chiefly structuring the vegetation by its abundant cover.
- Less represented species competing actively to occupy a position and coexisting with other species in the community. Their covers increase, decrease, or stabilize, depending on the ecological conditions prevailing in each post-fire dynamic stage.
- Several species present with a minimal cover, in all likelihood due to the strong competition pressures they undergo from the dominant taxa.

Table 7. Shannon-Wiener heterogeneity and equitability indices in the four sites with different fire intervals

Site N [Fire interval]	Site 1 [3 years]	Site 2 [6 years]	Site 3 [9 years]	Site 4 [12 years]
Heterogeneity	1.867 (±0.21)	1.843 (±0.10)	2.177 (±0.06)	1.963 (±0.12)
Equitability	0.660 (±0.06)	0.601 (±0.03)	0.698 (±0.01)	0.634 (±0.02)

Standard error between parentheses

Within the frame of the studied chronosequence, *Table 8* outlines the plant species dynamics as follow:

Table 8. Plant species dynamic in the four experimental sites

	Site 1 (3 years)	Site 2 (6 years)	Site 3 (9 years)	Site 4 (12 years)
<i>Asparagus aphyllus</i>	-	*	-	-
<i>Asphodelus aestivus</i>	**	**	-	-
<i>Atractylis gummifera</i>	**	*	-	*
<i>Blackstonia perfoliata</i>	*	*	-	-
<i>Brachypodium retusum</i>	**	**	*	*
<i>Calicotome villosa</i>	-	-	**	-
<i>Calicotome villosa</i>	-	-	-	**
<i>Cistus creticus</i>	***	***	***	***
<i>Dactylis glomerata</i>	-	*	*	**
<i>Drimia maritime</i>	-	*	-	*
<i>Gastridium ventricosum</i>	**	**	-	-
<i>Hypericum empetrifolium</i>	-	-	**	**
<i>Knautia integrifolia</i>	-	*	*	-
<i>Knautia integrifolia</i>	-	-	-	*
<i>Linum corymbulosum</i>	*	*	*	*
<i>Lotus angustissimus</i>	**	-	-	-
<i>Ononis spinosa</i>	-	*	-	-
<i>Origanum vulgare</i>	-	-	-	*
<i>Pidicaria dysenterica</i>	*	*	-	-
<i>Piptatherum miliaceum</i>	-	-	-	**
<i>Pulicaria dysenterica</i>	-	-	*	*
<i>Rhamnus lycioides</i>	*	-	-	-
<i>Sarcopoterium spinosum</i>	***	***	***	***
<i>Satureja thymbra</i>	**	**	-	-
<i>Tolpis virgata</i>	-	*	-	-
<i>Trifolium campestre</i>	**	**	*	*
<i>Trifolium physodes</i>	-	*	-	-

*** is a dominant species, ** is a less abundant species, * is a poor abundant species

Discussion

During the post-fire dynamic process, the fuel accumulated in the community was chiefly issued from shrubs, mainly made up of *Sarcopoterium spinosum* and *Cistus creticus*, and litter. Litter was enough accumulated as early as the 3rd post-fire year. In comparison with the results of Arianoutsou-Faraggitaki (1984) in a phrygana of Attica, there is an agreement about shrub dominance as soon as the 3rd post-fire year onwards. However, the community of Malaxa had almost double the shrub fuel load (3927.4 kg/ha vs. 1950.0 kg/ha) three years after the fire. Additionally, a total fuel load of the Malaxa phrygana in comparison with a *Sarcopoterium spinosum* dominated phrygana in Thessaloniki showed that the former had almost double fuel load (4673.9 kg/ha) than the latter (2800.0 kg/ha). Thus, the Malaxa phryganic community is characterized by a higher fuel production than the two other communities. These differences in biomass production may be attributed to differences in the prevailing environmental conditions or to the management practices (e.g., grazing), or even both.

It is important to highlight that the fuel characteristics favor particularly the high flammability of the vegetation. It seems clear that the high contributions of shrub and litter to the total fuel facilitate the spreading of any potential fire. The statement is based on (Specht et al., 2012) who reported that in shrub-dominated vegetation, the primary carrier of the fire is either shrubs or litter. Additionally, dead material accumulation with the age of the community is expressed by an increase of the dead-to-live fuel ratio, leading inevitably to an increase of the likelihood of fire and its potential intensity (Henkin et al., 1999; Seligman and Henkin, 2000; Paula et al., 2009). On the other hand, small sized fuel featuring phryganic dwarf shrubs, like *Sarcopoterium spinosum* and *Cistus creticus*, and its substantial accumulation with the age since the last fire, increase the vegetation flammability. According to Specht et al. (2012), small diameter fuel dries out and ignites more rapidly than larger fuel because of its large surface area compared to its volume. Consequently, fire most often starts and spreads in fine fuel.

Regarding the vegetation composition, it was noted that in Malaxa community shrubs contributed the bulk of the vegetation cover, while herbaceous plants were not abundant. This confirms previous observations about the encroachment potential of shrubs after a transitional competition by herbaceous plants during the first two post-fire years (Le Houerou, 1974; Naveh, 1974; Papanastasis, 1977; Arianoutsou-Faraggitaki, 1984; Keeley and Babr-Keeley, 1999). Shrub cover dominance in other Mediterranean-type shrublands has been exemplified by Ferran et al. (1998) who reported 76% of the total cover chiefly dominated by *Quercus coccifera* in garrigues of Valencia, three-and-a-half years after fire passage.

As far as the floristic composition is concerned, it was remarked that therophytes and hemicryptophytes were the dominant life forms (in terms of species number) in the studied community, with a noticeable advantage of the therophytes. Within the mentioned life form groups, by far, herbs prevailed over grasses. The comparison between the biological spectra of the studied phrygana and the grazed *Sarcopoterium spinosum* dominated batha of Ariel investigated by Ish-Shalom-Gordon (1993) shows that therophytes are, by far, the most represented life form with 49% and 56%, respectively. However, the two communities differed regarding the second highest represented life form; hemicryptophytes (27%) in Malaxa as against chamaephytes (15%; referred as bush by Ish-Shalom-Gordon) in Ariel. Geophytes were better represented in Ariel (12%) than in Malaxa (5%).

Furthermore, therophytes have been reported to be the most represented life form in other phryganic communities, but covering small areas (Bergmeier and Matthäs, 1996; Böhling and Gerold, 1995; Bergmeier, 1998; Ish-Shalom-Gordon, 1993) raised the possibility that the high annual therophytes richness portraying phryganic communities is favored by the occurrence of relatively predictable seasonal rainfall, but (Chilton and Turland, 2004) contended that the mentioned richness is the result of relatively rapid evolution under stress induced by drought, fire, and grazing. One has to note that due to their shallow-rooted system, therophytes depend on water supply in the upper soil layer to carry out their germination, growth, and reproduction (Bergmeier and Matthäs, 1996).

With respect to the floristic composition, the results obtained in Malaxa community are in agreement with those of Ish-Shalom-Gordon (1993) who recorded the same three dominant families in Ariel hatha: that is, Asteraceae, Fabaceae, and Poaceae. However, the two communities differed as regards the relative importance of the families: in Malaxa, the most represented family was the Fabaceae (22.8%), followed by the Poaceae (21.9%) and the Asteraceae (14.9%). On the contrary, in Ariel, the dominant family was the Asteraceae (16.6%), followed by the Fabaceae (14.6%) and the Poaceae (8.0%). The lower representation of Poaceae and Fabaceae in Ariel batha might be the fact of the higher grazing pressure (by goats and deers).

The richness values recorded in the studied phrygana cannot be fairly compared with the results obtained by other authors like Ish-Shalom-Gordon (1993) and (Bergmeier, 1997) who also investigated species richness in phrygana owing to the different methods used for data collection, and the management- types. For information, Ish-Shalom-Gordon (1993) found a total of 199 species in a grazed community of Ariel (Israel), using a 100 x 100 m plot; and Bergmeier (1997) counted a total of 91 and 86 species (and an average species number of 15.3 and 19.5) in grazed and non-grazed 20 x 30 microplots, respectively, in a phrygana of Sfakia (Crete). Nonetheless, the use of species richness as well as diversity indices provided a good insight into the organization of the community and the number of the more representative species at each post-fire stage.

The final interesting finding of the study is the similar stable species richness, heterogeneity, and equitability characterizing the community of Malaxa as early as the 3rd post-fire year onwards. These results are in line with other studies which indicated, that burned Mediterranean plant communities reestablish rapidly by auto succession process (Naveh, 1974; Trabaud and Lepart, 1980; Christensen, 1985; Trabaud, 1994; Arianoutsou, 1998; Henkin et al., 1999; Allen, 2014). Similar conclusions have also been drawn for Californian chaparrals (Trabaud and Lepart, 1980). However, the relatively low diversity characterizing the community of Malaxa, as compared to other more diversified phrygana, is in all likelihood due to both fire suppression and non-grazing.

Conclusions

The unburned and ungrazed phrygana is characterized by a rapid reestablishment of both vegetation cover and overall aboveground biomass. These two latter's are overwhelmingly dominated by highly flammable dwarf shrubs, chiefly *Sarcopoterium spinosum*, in the case at hand. The cover tends to close and stabilize as early as the 3rd post-fire year with little or no risk of soil erosion, whereas the overall aboveground

biomass needs a bit longer time to do so: that is, at the 6th post-fire year. In such a community, the herbaceous component is not substantially represented with respect to cover and aerial biomass (excepting during the first two post-fire years). This may be ascribed to the combination of both the high inhibiting competition pressure exerted by shrubs and the accumulation of litter, which restrict the spreading and the development of herbaceous plants to few openings which are temporarily free from competition.

Furthermore, the rapid reestablishment and stabilization of the representative species as well as the overall plant diversity as early as the 3rd post-fire year is in keeping with the general pattern of auto-succession and resilience characterizing Mediterranean-type communities which undergo cyclic fires. Phryganic communities recover faster than more advanced Mediterranean type shrublands. However, when the phrygana is ungrazed and unburned for a period, say 12 years as the community of Malaxa exemplifies it, the overall plant diversity becomes relatively low, probably after reaching its highest values during the first two post-fire years. Such a community may be characterized by a "dictatorial-type" organization (in which few species (chiefly dwarf shrubs in the present case), dominate by their abundances and broaden their niches to the detriment of the remaining species which are poorly represented.

In other respects, the conservation of the traditional practices, such as rotational burning and grazing, respectful of the diversity and the functioning of phryganic ecosystems may have positive socioeconomic repercussions. As previously, seen, a non-grazing situation associated with fire suppression for a period, both favor a rough encroachment of unpalatable dwarf shrubs such as *Sarcopoterium spinosum* and *Cistus creticus*, which heavily smother the herbaceous plants.

These are mainly annual legumes and grasses of high palatability and nutritive values. Consequently, the amount of pasture is reduced, and livestock production is lessened, affecting negatively the economy at both local and national levels. To optimize the benefits that can be gained from phryganic communities, both grazing and fire should be incorporated in the management plan, as pointed out by. To be beneficial, grazing management should observe a stocking rate equivalent to the grazing capacity of the rangeland, combine grazer and browser animals for a better control of plants, and respect the season and duration of grazing. Also, prescribed or controlled fires improve the grazing capacity of phryganic communities.

Tourism, as an additional source of income, can also be promoted by maintaining the biological and landscape diversity and attractiveness made up of mosaics of phrygana, maquis, and forests.

Post fire disturbances within the four study sites led to unpalatable and highly flammable dwarf shrubs, which smothered herbaceous plants. Species diversity was relatively low, indicating that few species crushingly structured the community by their high cover, while the remaining species were poorly abundant.

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