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MEDITERRANEAN DESERTIFICATION

A Mosaic of Processes and Responses

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9 Differing Responses of Greek Mediterranean Plant Communities to Climate and the Combination of Grazing and Fire

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1 INTRODUCTION

Patterns of distribution of world vegetation types have been studied since the beginning of the 19th century, particularly in relation to climate. Gradually the mechanisms through which climatic control is exercised have been determined, through the physiological responses of plants to climate factors (Woodward 1987).

Mediterranean-type ecosystems have received particular attention due to their pronounced seasonality, and possibly also due to their proximity to centres of population, now and through history. Such areas were considered ideal to study the notion of convergent evolution, not only studying the components (species) but extending the idea to the structure and function of the whole community (Mooney 1977; Conacher and Sala 1998). The concept is of course also applicable to other biomes that have evolved under other sets of similar macroclimatic conditions, such as the temperate forests or the tropical forests (both rainy and seasonal). It is expected, therefore, that under similar climatic conditions communities develop an analogous composition in terms of life forms.

Today in the Mediterranean region human intervention shapes the life-form composition of the present Mediterranean vegetation much more than natural forces do. This has been primarily through allowing grazing by livestock (and associated firing to enhance grasslands), and through agriculture, reforestation and any other mitigation schemes for the purpose of exploitation. Only very few plant species now share a common existence in areas having a Mediterranean-type climate on a world scale, so a direct species-by-species comparison is not possible. Nevertheless a suitable life-form classification scheme can offer a sound basis for inter-comparisons and the study of the match between communities and their environments (Begon et al. 1990).

The aim of the work described in this chapter was to compare the life-form composition of the vegetation in the MEDALUS I and II project sites with available data from two other Mediterranean-type areas of the world (i.e. California and Chile) with different land-use patterns and histories. The sites are listed in Table 9.1. It was expected that, under the same conditions, the growth-form composition of a community would be similar in sites with similar environmental conditions. The convergent evolution concept predicted that under similar environmental conditions plant species would develop similar adaptive traits (e.g. sclerophyll tissue). (In this chapter, 'life-form' and 'growth-form' are used synonymously.)

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Table 9.1 Landscape characteristics of MEDALUS I and II sites as well as some sites from California and Chile (Miller 1981)

Sites	Latitude	Elevation (m a.s.l.)	Annual precipitation (mm)	Mean annual temperature (°C)	Dominant vegetation type (local name)	Dominant plant growth forms[a]
California, USA						
Echo Valley	32°55′N	1000	476	13.4	Chaparral	Sev2-
Torrey Pines Park	32°35′N	110	200	15.8	Coastal sage scrub–chaparral–coastal pine	Ssc3- and Sscev2
Chile						
Fundo Santa Laura	33°04′S	1000	593	12.4	Matorral	Sev2 and Ssc3
Greece						
Hortiatis	40°36′34″N	400	440	16.2		Sev2
Petralona	40°21′38″	220	407	17.7		Sev2
Larissa	39°38′	73	466	16.2		Sev2 and desertified slopes
Spain						
Guadalentín Basin	39°00′	300	270	17.7		Tev2ndl, and S-2
Almeria (Rambla Honda)	37°07′55″	660	219.3	17.75		S-1, DS dc3 nal and GP
Murcia (El Ardal, Mula)	38°04′34″		266.4	17.15		
Sardinia (Olias, Santa Lucia)	39°11′18″	130	440.5	16.36		Sev2

[a]T, tree; S, shrub; DS, dwarf shrub; GA, grass annual; GP, grass perennial; HA, herb annual; HP, herb perennial; ev, evergreen; di, dimorphic; dc, deciduous; sc, semideciduous; 1, photosynthetic stem; 2, sclerophyllous; 3, malacophyllous; bdl, broad-leaved; nal, narrow-leaved; ndl, needle-leaved. For example, pine corresponds to Tev2ndl (tree, evergreen, sclerophyllous, needle-leaved).

2 METHODOLOGY

In the analysis, the Bray–Curtis ordination method was followed. It is an early ordination method but it remains efficient (Kent and Coker 1996). Each point on the resulting graph corresponds to a site, and distances between points on the graph reflect their similarities in terms of the factors controlling them (here it was the environmental parameters used and growth-form composition at each particular site). The Sorensen index was used as a similarity measure.

3 COMMUNITY STRUCTURE

The landscape characteristics most often used and assumed to have ecological implications or which have been useful in comparisons are presented in Table 9.1. A Bray–Curtis ordination diagram summarizes their similarities and differences (Figure 9.1). All the MEDALUS sites are grouped fairly closely together since they have similar properties. Almeria (southern Spain) is further apart, due to its more southerly position and climatic indexes. The American sites are also apart because of their lower latitudinal position and higher elevation (except Torrey Pines). In a Mediterranean region analogy these sites (Echo Valley and Fundo Santa Laura) are equivalent to sites somewhere in the Atlas mountains.

In Table 9.2 the life-form composition in each area is presented following the scheme of Stewart and Webber (1981). Two additional categories were used: the narrow-leaved sclerophyllous tree to accommodate the *Pinus* life forms and the drought-deciduous scrubs to accommodate the *phrygana* (e.g. coastal sage) formations.

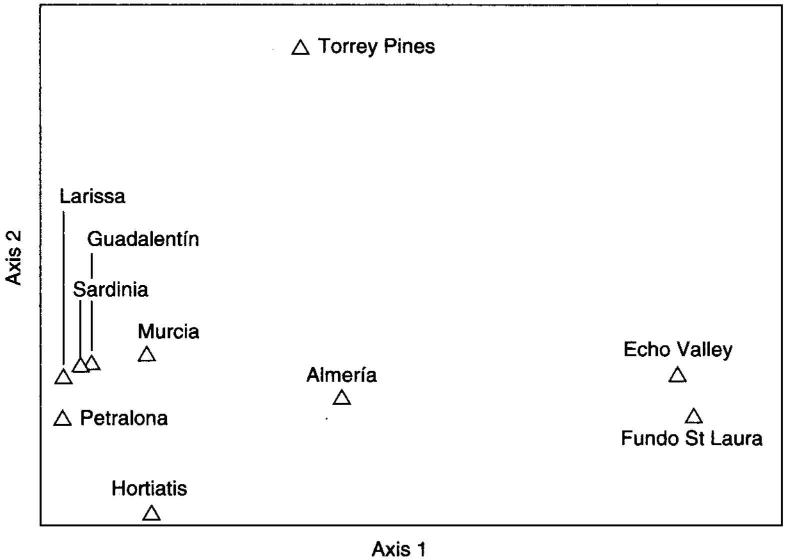

Figure 9.1 Two-dimensional plot of the study sites according to their land characteristics

Table 9.2 Cover per cent allocation between growth forms in seven MEDALUS and three American study sites. Categories are as described by Stewart and Webber (1981). Species named are the dominant species in these categories[a]

	Hortiatis	Petralona	Larissa	Sardinia	Murcia	Guadalentín	Almeria	Echo Valley	Torrey Pines	Fundo Santa Laura
Sev2bdl	65 Quco	45 Quco, Pile, Phla	50 Quco, Oleu, Phla	30	30	1 Quco		50 Qudu	20	60
Tev2ndl						25 Piha				
S(ev)2nal	20 Juox	10 Juox				20 Roof, Ancy		50		5
S-3bdl			70 Baac, Ciin	25				5	45	5
S-3nal							25 Ancy		20 Arca	20
Succulent								15	10	15
S-1							40 Resp			15

[a]Quco, *Quercus coccifera*; Pile, *Pistacia lentiscus*; Phla, *Phillyrea latifolia*; Oleu, *Olea europaea*; Qudu, *Quercus dumosa*; Piha, *Pinus halepensis*; Juox, *Juniperus oxycedrus*; Roof, *Rosmarinus officinalis*; Baac, *Ballota acetabulosa*; Ciin, *Cistus incanus*; Ancy, *Anthyllis cytisoides*; Arca, *Artemissia californica*; Resp, *Retama sphaerocarpa*.

Index of similarity according to Sørensen

$$Is = \frac{2c}{A + B}$$

where c is the number of species common to two releves or communities, A is the total number of species in releve (or community) A, and B is the total number of species in releve (or community) B (Mueller-Dombois and Hellenberg 1974).

Figure 9.2 is a Bray–Curtis ordination diagram summarizing the data of Table 9.2, where the sites are plotted according to the life-form composition of their vegetation. Visual comparison of Figures 9.1 and 9.2 shows that the use of the two different factors does not result in the same distribution of points on the graphs. This means that the two factors affect point distribution differently, and hence no strict relation exists between them (Dargie 1984). In Figure 9.1 MEDALUS sites are grouped fairly closely together. Here the difference in land uses and their effects on vegetation disperse the group. Almeria, with its extreme conditions which have a big impact on its vegetation, stays further apart.

Details of the alterations due to grazing have been studied at the species level for the association *Quercus coccifera–Stipa bromoides* and at the community level for the site at Larissa, in Greece. In evergreen sclerophyll formations between shrub patches the soil is covered by a large number of annual species and a few perennials, among which *Stipa bromoides* dominates. It forms rather large tussocks of tillers which grow up to 1 m in height and seem to occupy mainly the margins of the shrub patches. The maximum density of tussocks is found in the marginal zone and the minimum density under tall shrubs and in the uncovered soil. The spatial distribution of the tussocks is almost uniform in the marginal zone and aggregated in the uncovered areas as well as under the canopies of tall shrubs where a few micro-sites are available for *S. bromoides* to grow. The establishment and growth of the grass is facilitated at the margins where plants appear more robust (considering the height of the tillers and their number per tussock) and produce a large number of reproductive tillers.

Sharp gradients of light intensity, water and nutrient availability created across the transect from shrub clusters to the uncovered areas possibly explain the spatial arrangement of tussocks. For example, soil water potential at the surface soil layers is higher in the uncovered areas during midsummer (Table 9.3). Plants growing in such areas appear to be able to extract water and remain

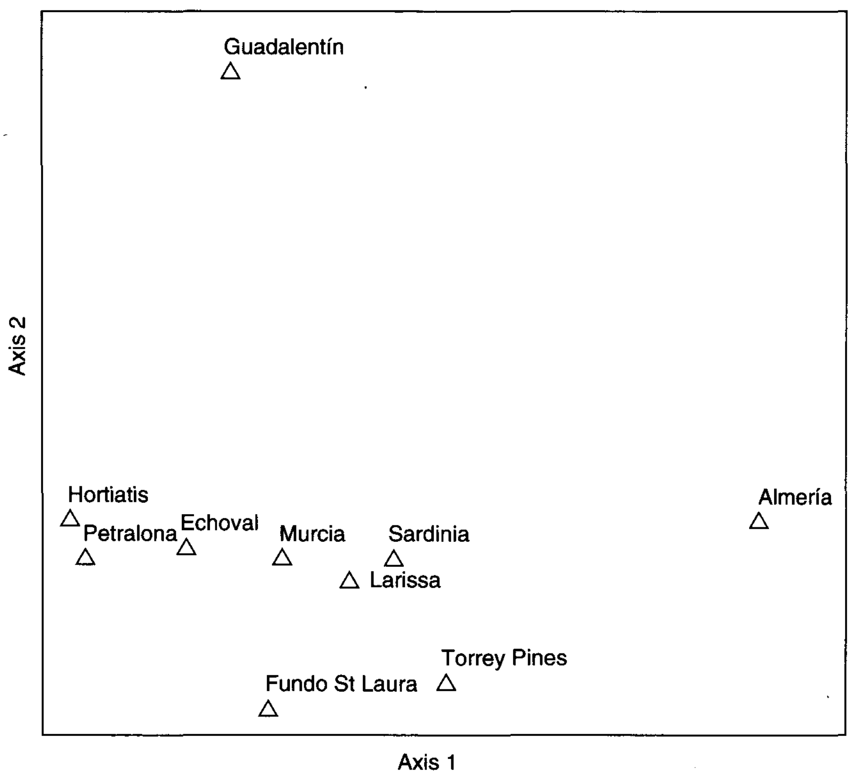

Figure 9.2 Two-dimensional plot of the study sites according to their life-form composition

Table 9.3 Values of water potential (in Mpa) for the soil and parts of *Stipa bromoides* inside and outside *Quercus coccifera* shrubs during August

	Inside shrub	Outside shrub
Soil	−4.58	−15.1
Roots	−17.8	−16.9
Stem	−24.6	−21.0
Old leaves	−25.3	−21.1
New leaves	−25.6	−24.7

active during summer but the cost of water extraction is greater than where plants are growing under the shrub canopies. So, inside shrubs of 30 cm height we can count 2.31 tiller m^{-2}. This number decreases to 1.68 inside higher shrubs (60–70 cm) but reaches a maximum at the shrub periphery (2.76), while being only 0.72 in open spaces. Greater levels of nitrogen in the marginal zone may also facilitate the growth of the plants at this specific site. By growing in the marginal zone and under the canopies of low shrubs, *S. bromoides* avoids competition from the fast-growing annuals for nutrients, and competition from *Q. coccifera* for light. It also avoids, to a certain degree, the effects of trampling during the establishment phase.

Under grazing pressure and depending on its intensity, which varies in time and space, the shrub boundaries and height are in a dynamic state of expansion and shrinkage. Grazing, at a certain moderate level, facilitates the establishment and growth of *S. bromoides*. In the absence of grazing, the growth of *Q. coccifera* canopies and grasses is expected. In overgrazed areas the abundance of different species is expected to diminish since soil conditions will cease to be favourable.

4 FUNCTIONAL TRENDS

4.1 Response to Nutrients

Availability of nutrients might affect the presence or absence of particular life forms. For this reason levels of nitrogen and phosphorus were studied at different sites, as well as their interaction with particular life forms. At the Hortiatis (Greece) site, the pattern of nitrogen (N) and phosphorus (P) circulation between soil and *Quercus coccifera* shrubs was studied. The N content in the tissues was greater during the growing period and there was no direct correlation of N with temperature and humidity. The study of the N distribution in different plant parts (leaves, wood, fine and large roots) and in three categories of plants, i.e. heavily, moderately and non-grazed, as well in the soil, showed that N concentration increases simultaneously in the soil and the grazed shrubs while showing a time lag in the non-grazed shrubs. The reason for this delay might be attributed to the larger leaf mass in the non-grazed shrubs.

Unlike nitrogen, the phosphorus distribution in the *Q. coccifera* tissues is controlled by a combination of temperature and humidity, and shows significant differences between autumn–winter and spring–summer samples.

5 LAND USES

5.1 Disturbance Regime

Extensive grazing and fires are the main disturbance factors in all Mediterranean areas of the world. Although some authors (Stewart and Webber 1981) consider that in California urbanization is the biggest threat to the chaparral vegetation, the same cannot be said for the Mediterranean region itself. The combined effect of grazing and fire leads to communities where as the grazing pressure increases along with the frequency of fire, total biomass is reduced and the evergreen broad-leaved sclerophyllous species are replaced by thistles and annual grasses. The results of this study are summarized in Table 9.4, according to the species participating in each group. Taking the growth forms percentage in each group, it was observed that the effect of grazing shifted the character of the community from a shrubland to a prairie. Grouping of specimens from each sampling site gave the community types presented in Table 9.4 in terms of species composition. The Sørensen similarity index is given in Table 9.5.

Figure 9.3 shows the pathways of degradation. Community 1 is more or less the climax stage. Light grazing opens up the closed structure and leads to Community 2. From this stage combinations of fire frequency and fire intensity follow either the path from Communities 5 and 6 to Communities 7 and 9 or through Communities 4 and 3 to Community 8. As can be seen from Table 9.4, Communities 8 and 9 are dominated by annuals or perennial herbaceous species and grasses.

The effects of grazing on shrub morphology, seed ecology and herb layer have been studied also by Puigdefabregas (1999) for the dwarf shrub *Anthyllis cytisoides* (classified as narrow-leaved sclerophyllous scrub). The herb layer under and between *Retama* has been studied and results showed that the responses to grazing level were significant only if grazing was held constant throughout a bush's life. Also, grazing had no impact on seed production, or the seedling development of the shrub. The effects of grazing on the herb layer led to the dominance of species associated with open semi-arid environments, as expected.

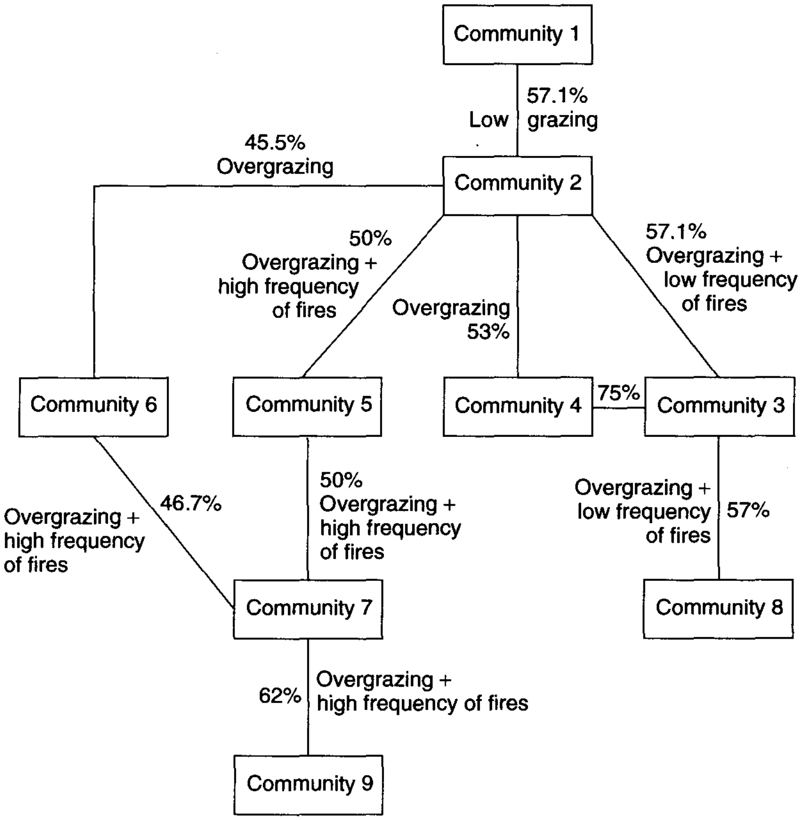

Figure 9.3 Diagrammatic representation of the degradation paths followed, according to the intensity of grazing and fire frequency

Table 9.4 The plant species occurring in each of the nine communities that can be distinguished along a fire-grazing intensity gradient

Plant species	Growth form	Communities								
		1	2	3	4	5	6	7	8	9
Quercus coccifera	EBLSS	+	+				+			
Olea europaea	EBLSS	+					+			
Cistus incanus	BLMDS	+	+							
Thymus capitatus	NLSDS	+	+		+					+
Helianthemum sp.	NLSDS	+								
Asphodelus aestivus	PH	+	+	+	+	+				
Asparagus acutifolius	PThistle	+					+			
Ballota acetabulosa	BLMDS	+	+				+			
Pterocephalus papposus	H	+	+			+		+		
Crataegus sp.	DTree	+								
Dactylis glomerata	G	+				+				
Phillyrea latifolia	EBLSS	+								
Poa sp.	H	+						+		
Chrysopogon gryllus	G	+								
Eryngium campestre	AT		+	+	+		+	+	+	+
Euphorbia cf. myrsinites	ENLDS		+		+	+				
Carlina vulgaris	AT		+	+		+	+	+	+	+
Bupleurum glumaceum	HNL		+			+		+		
Trifolium sp.	H		+			+	+	+		+
Aegilops sp.	AG		+							+
Eryngium creticum	HThistle		+	+				+		+
Teucrium polium	ENLMDS			+	+	+				
Scolymus hispanicus	PScrub				+					
Pyrus amygdaliformis	DTree					+	+	+		
Thymus striatus	Scrub					+	+	+	+	+
Petrorhagia sp.	HNL					+	+	+		+
Anthemis sp.	H					+		+		
Avena sp.	AG					+		+		
Tordyllium sp.	ABL					+		+		
Allium sphaerocephalon	PBL					+				
Hordeum sp.	AG					+				
Phalaris sp.	PG					+				
Paliurus australis	Scrub						+		+	
Melica sp.	AG						+			
Taeniatherum caput-medusae	G						+			
Sideritis curvidens	H							+		
Nigella sp.	H							+		+
Cynodon dactylon	AG							+		
Lagurus ovatus	AG							+		+
Centaurea sp.	H							+		
Bromus sp.	AG							+		
Sonchus sp.	H							+		+
Carlina sp.	AT							+		
Euphorbia sp.	NLSDS							+		
Vulpia sp.	H							+		

(continued overleaf)

Table 9.4 *(continued)*

Plant species	Growth form	Communities								
		1	2	3	4	5	6	7	8	9
Silybum merianum	AT									+
Marrubium peregrinum	Scrub, hairy leaves									+
Verbascum sp.	H									+
Alyssum sp.	H									+

EBLSS, evergreen broad-leaved sclerophyllous shrub; BLMDS, broad-leaved malacophyllus deciduous scrub; NLSDS, narrow-leaved summer deciduous shrub; PH, perennial herb; AG, annual grass; ABL, annual broad-leaved; PBL, perennial broad-leaved; PG, perennial grass; AT, annual thistle; ENLDS, evergreen narrow-leaved dwarf scrub; ENLMDS, evergreen narrow-leaved malacophyllus dwarf scrub; A, annual; P, perennial; H, herbaceous; G, grass; D, deciduous

Table 9.5 The values of the Sørensen similarity index for the communities described in Table 9.4 based on species composition

	Com. 1	Com. 2	Com. 3	Com. 4	Com. 5	Com. 6	Com. 7	Com. 8	Com. 9
Com.1	57.1%	11%	22%	21.4%	33.3%	5.5%	0%	7.1%	
Com.2	57.1%	53%	50%	45.5%	32.3%	26.7%	43.5%		
Com.3	75%	31.6%	23.5%	24%	57.1%	35.3%			
Com.4	30%	10.5%	7.1%	22%	21%				
Com.5	38.5%	50%	21.1%	20.1%					
Com.6	46.7%	40%	42%						
Com.7	25%	62%							
Com.8	37.5%								
Com.9									

5.2 Reforestation

As grazing and fire (especially fire) represent powerful means of changes in the plant species and accordingly the growth-form composition in any given community, it was judged useful to study the impact of mitigation schemes, specifically reforestation. Reforestation represents another way in which the life-form composition of an area can be changed, though this time with good intentions. Results from a census of 12 reforested areas in mainland Greece are presented in Table 9.6. They show that species number, species diversity and evenness in natural ecosystems of broad-leaved sclerophylls are higher than in reforested areas, and suggest that these communities in continental Greece are well established, with remarkable homogeneity in their structural characteristics, independent of the management practices that were applied at each site.

However, in the reforested areas, the values of the community characteristics are significantly lower than those in the *maquis* ecosystems, revealing the presence of immense differences in the community structure of these two types of ecosystems. Factors interacting include the species used in reforestation and the year of plantation. In addition, species number, species diversity and evenness in the reforested areas decrease as time from the year of plantation passes, since strong dominance of the pine species leads to the extinction, under their canopy, of most of the other woody species. Thus, minimum values of the above-mentioned community structure parameters are observed in the oldest plantations. This indicates that with reforestation, as a restoration practice, simplified ecosystems are developed, strongly differing in species composition and structure from the initial natural vegetation. Even if in the first years of reforestation there exist similarities between the two types of ecosystems (*maquis* and reforestation), as time passes their divergence gradually increases, resulting in two different ecosystems after 70–80 years.

Table 9.6 Results of the census in 12 reforested areas in mainland Greece and the neighbouring community of evergreen broad-leaved sclerophylls. The year is the date of reforestation. Indexes used are species number (S), Shannon-Wiener (H') and Evenness or Pielou (J)

Sites	Year	Evergreen broad-leaved			Reforestation		
		S	H'	J	S	H'	J
Nafpaktos	1914	8	1.67	0.81	3	0.29	0.26
Nafpaktos	1948	"	"	"	4	0.80	0.31
Atalante	1928	8	1.69	0.81	3	0.31	0.29
Atalante	1936				3	0.33	0.30
Ermione	1965–1966	12	1.53	0.62	8	1.07	0.52
Tristinika	1979	8	1.84	0.89	7	1.48	0.76
Taygetos	1951	9	2	0.91	3	0.27	0.24
Rapsani	1957	8	1.47	0.71	4	0.25	0.18
Polygyros	1970	10	1.66	0.72	5	0.62	0.39
N Marmaras	1974	12	1.78	0.72	4	0.87	0.63
Stylida	1937	8	1.63	0.78	5	0.64	0.4
Stylida	1953				6	1.04	0.58
Kavala	1945–1947	11	2.08	0.87	6	0.94	0.52
Basilica	1958	12	1.83	0.74	3	0.15	0.13
Basilica	1966			2	0.2	1	0.30
Mt Pelion	1970	12	1.78	0.72	8	1.24	0.60

6 CONCLUSIONS

The concept of convergent evolution of species under similar environmental conditions was used in order to evaluate the evolution of Mediterranean plant communities, especially those in Greece. In the case of communities, the growth-form composition was used, instead of species characteristics. The Bray–Curtis polar ordination method was used and the per cent participation of growth forms in its composition was used to show community characteristics. Ordination of sites according to their environmental characteristics produced different results from when the growth-form composition basis was used. This finding persisted when examining sites at a global, regional or local level. So, while specific characteristics at the level of species seem to converge, at the community level the growth-form composition may vary considerably.

The impacts of grazing and fire on soil nutrients and community composition were investigated. Results showed that while grazing affected mainly individual species (such as the shrub *Quercus coccifera*) it was fire or "corrective actions" such as reforestation that changed species composition and altered the community status. Also, the duration of that action rather than specific environmental parameters seemed to be the cause of divergence between communities. This indicates how carefully land use has to be planned when acting to reverse desertification (Thornes and Brandt 1997).

Further work on the life-form classification and participation in the structure of the vegetation in an area can help us gain a better understanding of the relationship between vegetation and environmental conditions, in the inter-comparisons between areas of the Earth geographically apart but having the same macroclimate (Oechel et al. 1981). Such inter-comparisons are useful, especially for the Mediterranean region itself since the intensity of the land use over the centuries has profoundly changed the natural vegetation and its supporting landscape. Life-form structure may be the common link for a better design of the corrective measures and the exploitation practices that are needed.

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