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Long-term post-fire vegetation dynamics in *Pinus halepensis* forests of Central Greece: A functional group approach

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Abstract

A hierarchical approach for plant functional classification was applied to describe long-term vegetation change in *Pinus halepensis* burned forests. Plant species were initially grouped according to their growth form and afterwards data on species modes of regeneration, persistence and dispersal, together with some other specific competitive advantages were explored, resulting in the identification of 29 different functional groups, 14 for woody and 15 for herbaceous species. Three types of *Pinus halepensis* forests were identified, according to the structure of the understorey. For each forest type, a post-fire chronosequence of communities was selected for sampling. Data sampling was performed for at least two consecutive years in each community, so as to reduce the shortcomings of the synchronic approach and to increase the age range of each chronosequence. Even though the vast majority of the functional groups proved to be persistent throughout the post-fire development of vegetation, their species richness and abundance did not remain stable. An increase of annual herb richness and abundance was recorded in the first years after the fire, with the leguminous species forming the dominant functional group. For perennial herbs, the most abundant group was of species with vivid lateral growth, while the group of species with subterranean resource organs included the highest number of species. Finally, as far as the woody species are concerned, the groups that played the most important role in defining vegetation structure were the mono-specific group of the pine, the group of resprouting sclerophyllous tall shrubs and the group of obligate seeder short shrubs (with *Cistus* spp., among others). A negative relationship between the abundance of woody obligate resprouters and the regeneration of woody obligate seeders was found. The advantage of the proposed functional group approach over classical floristic or structural approaches for the long-term study of communities is discussed, together with the applicability of this approach in studies of vegetation risk assessments due to fire regime alterations.

Introduction

Fire, the major natural disturbance in pine forest ecosystems throughout the world (Mirov 1967; Attiwill 1994; Richardson and Rundel 1998), is an important factor for the maintenance of structure and biodiversity of *Pinus halepensis* Mill. forests (Walter 1968; Naveh 1994; Arianoutsou 2001). The fire regime of these ecosystems is characterized by high intensity fire events (Agee 1998), with an average occurrence interval of approximately 30 to 50 years (Arianoutsou 2002). Plant species inhabiting these ecosystems have evolved under the influence of the respective fire regime, having all the necessary biological attributes that enable them to be fire resilient (Arianoutsou and Ne'eman 2000; Trabaud 2000; Grove and Rackham 2001).

It has been proposed that the autoecological approach to resilience would be the most promising one for developing predictive indices of community response to disturbance (Keeley 1986). In the case of *P. halepensis* forests, where full recovery requires more than 30 years (Kazanis and Arianoutsou 1996; Schiller et al. 1997; Trabaud 2000; Arianoutsou and Ne'eman 2000), species resilience does not depend only on their early response to fire. Traits that define long-term recovery species presence and performance should be also taken into consideration. Therefore, apart from regeneration mode, data on species mode of persistence through vegetation development, dispersal from adjacent stands and competition potential are required for understanding and predicting community response to disturbance. Given the practical problems existing in acquiring the detailed knowledge of the autecology of all species included in any plant community, the identification of functional groups in regard to disturbance would be a useful tool (Pausas 1999a; Arianoutsou 2002), particularly since a minimum set of critical traits is required (Campbell et al. 1999).

Although there is a great deal of published information on the initial stages of post-fire recovery of *P. halepensis* forests (Trabaud et al. 1985a; b; Kutiel and Kutiel 1989; Ne'eman et al. 1992; Papavassiliou and Arianoutsou 1993; Thanos et al. 1996; Herranz et al. 1997), there is a characteristic absence of data on plant species long-term recovery pattern. The available, short-term data correspond to diachronic records of several consecutive years after fire, which is practically impossible for long-term studies. On the other hand, chronosequence studies (synchronic approach) provide evidence on the presence and abundance of species in various post-fire ages (Kazanis and Arianoutsou 1996; Schiller et al. 1997) but little, if any, information can be derived for species performance (establishment, growth and senescence) on a year-to-year basis.

Consequently, a sampling design that combines the synchronic and diachronic approaches should be the solution in order to relate long-term vegetation change and species performance. This paper reports on long-term post-fire vegetation dynamics in *P. halepensis* forests of Central Greece with data acquired from a sampling design of this kind. All traits defining species resilience to fire have been explored and allowed the description and analysis of vegetation dynamics through a functional group classification system.

Materials and methods

Study sites

Three types of *P. halepensis* forests are found in Central Greece (Kazanis and Arianoutsou 2002). The first type (Type A) corresponds to forests with dense, well-developed woody understorey, dominated by evergreen sclerophyllous species, such as *Quercus coccifera* L., *Arbutus andrachne* L. and *Phillyrea latifolia* L. Forests of this type are mainly found at remote areas, where human influence is minimal, such as in several locations of Mt. Parnies National Park. The second type (Type B) consists of forests located near the forest-urban interface, with the woody understorey being less developed than in type A, but still dominated by sclerophyllous evergreen shrub species, such as *Q. coccifera* and *Ph. latifolia*. Whereas the first two *P. halepensis* forest types correspond to forests of the mountainous zone, the third one is distributed on slopes or plains of low elevation, usually not far from the seashore. This third type (Type C) is of forests with sparse, open woody understorey that is dominated by dwarf shrubs, such as *Coridothymus capitatus* (L.) Rchb, *Phagnalon graecum* Boiss. & Heldr. and *Helichrysum stoechas* (L.) Moench.

For each one of the three forest types, a chronosequence of pine communities was considered for sampling (Table 1). The criteria for selection of these communities were the availability of data on fire history, a minimum post-fire human intervention and the inclusion of as many post-fire age classes as possible. Effort was made to include communities of similar ages in all three chronosequences, but this was not always possible.

Sampling design

In the context of this study, each plant community is defined as a particular stand of a pine forest that is developed on a slope characterized by the combination of several environmental variables (altitude, aspect, steepeness, stoniness, pH, soil texture, meteorological conditions). Plant community composition was analyzed with the application of the line transect sampling method, that is more advantageous over the traditional plot sampling method since it allows the survey of a larger part of the community at a minimum time (Brower et al. 1990). Three 50-m-long line transects were established in each community. The initial point of each transect was defined randomly. The three transcets had different directions and were located at least 25 m apart, so as to sample the maximum of the community in question.

All plants, either growing along the transects or having their canopy intercepted by them were recorded. Data recording was performed three times per year (October-November, February-March, May-June) so as to include autumnal and winter species

Table 1. Characteristics of the sites where the studied communities are found. Communities are arranged with increasing post-fire age and grouped according to the respective pine forest type. The age of the unburned (mature) stands was estimated by measuring the annual growth rings of the pine trees.

Site	Prefecture	Fire event	Post-fire age	Parent-rock material	Altitude	Sampling period
Type A						
Loutsa	Dirfy Mountain, Euboia	1994	1–4 yrs	Limestone	350 m	10/1994–6/1995
Fyli	Parnes Mountain, Attica	1989	8–9 yrs	Limestone	410 m	10/1996–6/1998
Belletsi	Parnes Mountain, Attica	1982	13–16 yrs	Limestone	590 m	10/1994–6/1998
Bahounia	Parnes Mountain, Attica	1980	17–18 yrs	Schists	660 m	10/1996–6/1998
Agios Merkourios	Parnes Mountain, Attica	–	>65 yrs	Schists	580 m	10/1994–6/1998
Type B						
Mavrinora	Penteli Mountain, Attica	1995	1–3 yrs	Schists	420 m	10/1995–6/1998
Agios Stefanos	Penteli Mountain, Attica	1993	2–4 yrs	Tertiary Deposits	310 m	10/1994–6/1997
Stamata	Penteli Mountain, Attica	1991	5–8 yrs	Schists	405 m	10/1994–6/1998
Fyli	Parnes Mountain, Attica	1989	8–9 yrs	Schists	410 m	10/1996–6/1998
Dionysos	Penteli Mountain, Attica	1982	13–16 yrs	Schists	460 m	10/1994–6/1998
Pontos	Penteli Mountain, Attica	–	>55 yrs	Schists	380 m	10/1996–6/1998
Type C						
Pikermi	Mesogeia Plain, Attica	1995	1–2 yrs	Tertiary Deposits	180 m	10/1995–6/1997
Kamariza	Sounion Peninsula, Attica	1985	12–13 yrs	Schists	185 m	10/1996–6/1998
Kamariza	Sounion Peninsula, Attica	1985	12–13 yrs	Limestone	185 m	10/1996–6/1998
Pikermi	Mesogeia Plain, Attica	1978	17 yrs	Tertiary Deposits	190 m	10/1994–6/1995
Markati	Sounion Peninsula, Attica	-	>55 yrs	Schists	180 m	10/1996–6/1998

with a very short period of activity, too. Based on these records species richness and species abundance were evaluated for each community per year of sampling. For the majority of the herbaceous species, which had different values of linear density among the autumnal, winter and spring samplings, the maximum value was taken into consideration.

Furthermore, several records were taken regarding species biological traits (growth form, life form, regeneration mode, dispersal mode) which were needed for the application of the functional group classification system.

Functional groups classification

All biological attributes that were taken into consideration for the application of the long-term post-fire functional group classification system are given in Table 2. The classification was done in a hierarchical way, with all species being initially grouped according to their growth form. It should be mentioned that the growth form that was recorded for several woody species was different from their potential growth form reported in other habitats. For the current analysis, species were classified according to their actual and not the potential growth form.

From that point on, all biological traits determining the pattern of species presence and abundance throughout the post-fire community development were considered. Such biological traits were: the regeneration mode, the mode of persistence, the dispersal mode and, finally, several characteristics that may provide some groups of plants with specific competitive advantages. In the literature, a given species may quite often be referred either as obligate seeder or as a facultative resprouter, depending on the geographical region or the type of habitat (see Pausas 1999a; Seligman and Henkin 2000 for some examples). Differences in fire intensity or climatic conditions may account for this. Thus, similarly with what was mentioned before, only the regeneration mode observed in the field during the current and other studies made by the authors in the same habitats were taken into account for each species.

Table 2. Biological attributes considered for the classification of the recorded plant species in functional groups.

Growth form	Regeneration mode	Mode of persistance	Long distance dispersal mode	Specific competitive advantage
Tree				
Tall shrub	Obligate resprouter	Long life span		Nitrogen fixation
Short shrub	Obligate seeder	Secondary seedling establishment	Anemochorous	Subterranean storage organs
Woody liana	Facultative seeder	Soil seed bank	Zoochorous	Vivid lateral growth
Perennial herb	Colonizer	Long distance dispersal	None	Parasite
Annual herb				None

Nomenclature

Plant nomenclature follows Med-Checklist (Greuter et al. 1984-1989) and Flora Europaea (Tutin et al. 1981-1993) for the families not included in the published volumes of Med-Checklist.

Results

In the context of this study 296 species were recorded. Effort was made to classify each species to a functional group according to its relevant biological attributes. Twenty-one (21) species remained unclassified, as no evidence of their regeneration mode was detected. These species were recorded in communities of older age, a result probably indicating the absence of a specific regeneration mode, but this hypothesis cannot be supported. Species classification resulted in twenty-nine (29) functional groups, fourteen (14) for woody and fifteen (15) for herbaceous species. Species biological attributes within each group are given in Table 3. Each functional group has been named after one of the most typical species of the respective group. A complete list of all the species classified per functional group can be found in the Appendix.

Six growth forms of plants were encountered: trees, tall shrubs, short shrubs (maximum 1-m-tall), woody lianas, perennial and annual herbs. Tree species were classified into two functional groups. The first group is a mono-specific one, with the obligate seeder *P. halepensis* being its only member. The second group includes tree species of the Rosaceae (*Crataegus monogyna* Jacq., *Pyrus communis* L.) and the Fagaceae (*Quercus ilex* L., *Quercus pubescens* Willd.) families that regenerate only by resprouting and which grow sparsely in the understorey of the pine forest.

Three functional groups were distinguished among the tall shrub species. The *Quercus coccifera* group consists of evergreen sclerophyllous species that are obligate resprouters. The *Calicotome villosa* (Poir.) Link group includes tall, usually spiny, leguminous shrubs that primarily regenerate by seedling establishment but resprouting has also been recorded. Finally, the third group is a mono-specific group with *Juniperus phoenicea* L., a tall gymnosperm that cannot regenerate after fire, and consequently its re-establishment depends on factors related to its dispersal ability (presence of mature individuals in the proximity of the burned stand, presence of dispersing birds). All woody lianas share similar biological attributes in relation to fire and postfire vegetation development, forming a single functional group, the *Smilax aspera* L. group.

Short shrubs are a heterogeneous group with species characterized by a variety of biological attributes. There is a group of obligate resprouters (*Asparagus acutifolius* L.group) and two groups of facultative resprouters, the first consisting of species with long life span (*Erica manipuliflora* Salisb. group) whereas the other group includes species that require secondary establishment in order to ensure their persistence (*Hypericum empetrifolium* Willd. group). In other words, species of the latter functional group have short life span and when the senescence of the post-fire established individuals occurs, species persistence is achieved by the establishment of new individuals in the absence of fire.

The last five functional groups of short shrub species rely on post-fire seedling establishment for their regeneration. The difference between these groups deals mainly with the temporal pattern of post-fire seedling establishment. The majority of species are established during the first year after the fire event (obligate seeders, *Genista acanthoclada* DC., *Dorycnium hirsutum* (L.) Ser. and *Cistus salvifolius* L. groups). Still, there are some species that do not become established earlier than the second post-fire year. These

Table 3. Biological attributes characterizing the species classified in each functional group. Different groups are named after a typical species.

Typical Species	Symbol	Growth form	Regeneration mode	Mode of persistance	Long dispersal mode	Specific competitive advantage
Pinus halepensis	Phal	Tree	Obligate seeder	Long life span	Anemochorous	None
Crataegus monogyna	Cmon	Tree	Obligate resprouter	Long life span	Zoochorous	None
Quercus coccifera	Qcoc	Tall shrub	Obligate resprouter	Long life span	Zoochorous	None
Calicotome villosa	Cvil	Tall shrub	Facultative resprouter	Long life span	None	Nitrogen fixation
Juniperus phoenicea	Jpho	Tall shrub	Colonizer	Long dispersal mode	Zoochorous	None
Smilax aspera	Sasp	Liana	Obligate resprouter	Long life span	Zoochorous	None
Asparagus acutifolius	Aacu	Short shrub	Obligate resprouter	Long life span	Zoochorous	None
Erica manipuliflora	Eman	Short shrub	Facultative resprouter	Long life span	Anemochorous	None
Hypericum empetrifolium	Hemp	Short shrub	Facultative resprouter	Secondary establishment Long dispersal mode	Anemochorous	None
Genista acanthoclada	Gaca	Short shrub	Obligate seeder	Long life span Soil seed bank	None	Nitrogen fixation
Dorycnium hirsutum	Dhir	Short shrub	Obligate seeder	Secondary establishment Soil seed bank	None	Nitrogen fixation
Cistus salvifolius	Csal	Short shrub	Obligate seeder	Secondary establishment Soil seed bank	None	None
Coridothymus capitatus	Ccap	Short shrub	Delayed seeder	Secondary establishment	None	None
Phagnalon graecum	Pgra	Short shrub	Colonizer	Long dispersal mode	Anemochorous	None
Cyclamen graecum	Cgra	Perennial herb	Obligate resprouter	Long life span	Unclear	Subterranean resource organs
Brachypodium pinnatum	Bpin	Perennial herb	Obligate resprouter	Long life span	Anemochorous Zoochorous	Vivid lateral growth
Centaurea mixta	Cmix	Perennial herb	Obligate resprouter	Long life span	Anemochorous	None
Convolvulus elegantissimus	Cele	Perennial herb	Facultative resprouter	Long life span Soil seed bank	None	None
Bituminaria bituminosa	Bbit	Perennial herb	Obligate seeder	Secondary establishment Soil seed bank	Zoochorous	Nitrogen fixation
Ajuga chamaepitys	Acha	Perennial herb	Obligate seeder	Secondary establishment Soil seed bank	None	None
Stachys cretica	Scre	Perennial herb	Delayed seeder	Secondary establishment	None	None
Scabioza columbaria	Scol	Perennial herb	Colonizer	Long dispersal mode	Anemochorous, Zoochorous	None
Cytinus hypocistis	Chyp	Perennial herb	Delayed resprouter?	Long life span	Anemochorous?	Parasite
Lathyrus cicera	Lcic	Annual herb	Obligate seeder	Secondary establishment Soil seed bank	Zoochorous	Nitrogen fixation
Tuberaria guttata	Tgut	Annual herb	Obligate seeder	Secondary establishment Soil seed bank	None	None
Hypochoeris achyrophorus	Hach	Annual herb	Obligate seeder	Secondary establishment	Anemochorous Zoochorous	None
Biscutella didyma	Bdid	Annual herb	Delayed seeder	Secondary establishment	None	None
Aira elegantissima	Aele	Annual herb	Colonizer	Long dispersal mode	Anemochorous Zoochorous	None
Cuscuta epithymun	Cepi	Annual herb	Colonizer?	Long dispersal mode	Zoochorous	Parasite

are usually members of the Compositae (*Phagnalon graecum* Boiss. & Heldr., *Helichrysum stoechas* (L.) Moench) and the Labiatae (*Coridothymus capitatus*, *Micromeria nervosa* (Desf.) Benth.) families. In the first case, the species are anemochorous and they become established only after their dispersal units arrive in the burned stand from adjacent unburned patches (colonizers). Species of the second case are either achorous or autochorous and consequently they can not have their dispersal units dispersed over long distances. Thus, it is reasonable to assume that their seedlings are produced by seeds that remain in the burned soil and for some reason they do not germinate during the first post-fire year. This is the reason why we characterized them as "delayed seeders".

Both perennial and annual herbs are quite diverse in their response towards fire, as it can be derived from the number of different functional groups that correspond to each growth form. Out of the 9 functional groups of perennial herbs, 3 refer to obligate resprouters. The *Cyclamen graecum* Link group includes species with subterranean storage organs (bulbs, rhizomes). The *Brachypodium pinnatum* (L.) P. Beauv. group consists of species that show vivid lateral growth, providing themselves with strong competitive ability against other species. All the other perennial herbs that regenerate only by vegetative means are members of the *Centaurea raphanina* Sibth. & Sm. group. Perennial herbs that regenerate both by resprouting and seedling establishment form the *Convolvulus elegantissimus* Mill. group.

In a way similar to what was described for the short shrubs, perennial herbaceous species that regenerate only by seedling establishment were organized in four groups: *Bituminaria bituminosa* (L.) Stirton (the leguminous) and *Ajuga chamaepitys* (L.) Schreb. (the non-leguminous) groups of species establishing the first year after fire, *Stachys cretica* L. group for the "delayed seeders" and *Scabiosa columbaria* L. group for the colonizers. A last group of perennial herbs is the *Cytinus hypocistis* (L.) L. group that consists of parasitic herbs which appear vegetatively only after the populations of the host-species have reached a peak. Typical is the case of *Cytinus hypocistis*, a root-parasite of *Cistus* spp., which sprouted only after the third post-fire year when its host plant species dominated the vegetation. Consequently, we have characterized these species as "delayed resprouters".

Annual species, which are all dependent on seedling establishment for post-fire regeneration, are divided into 6 groups. The 3 first groups refer to species that establish during the first post-fire year. These are the *Lathyrus cicera* L. group (annual legumes), the *Tuberaria guttata* (L.) Fourr. group (including species without long dispersal mode) and the *Hypochoeris achyrophorus* L. group (including species with long dispersal mode). Furthermore, there is a group of "delayed seeders" (*Biscutella didyma* L. group) and two groups of "colonizers" (*Aira elegantissima* Schur. and *Cuscuta epithymum* (L.) L. group).

In Table 4, the number of recorded species per functional group is given for the overall chronosequence of all studied communities but also for each one of the secondary chronosequences that correspond to the three types of *Pinus halepensis* forests. Two groups of annual herbs (*Lathyrus cicera* and *Aira elegantissima* groups) were found to have the highest number of species, followed by the perennial herbaceous *Cyclamen graecum* group. Among the woody groups, the highest number of species (with the exception of the Type C chronosequence) was classified in the *Quercus coccifera* group. The example of the latter group emphasizes the fact that not all functional groups were equally represented among the three community types. As a matter of fact, there are groups with no representatives in one or two of the community types (Table 4). In general, the highest functional group richness was recorded in the communities of Type B, while the lowest in the Type C communities.

Apart from the recorded differences in the species number of various groups among different types of communities, differences were also encountered within the same community type but with differing post-fire age. For perennial species (both woody and herbaceous) these differences were minimal and mainly related to initial floristic composition of each community and not to post-fire age. It was the annual species component that showed the most dynamic long-term pattern, as it can be seen in Figure 1, where data are presented separately for the five functional groups with the highest overall species number (Table 4). Results are arranged separately for each one of the three identified types of pine forest, with the presented data been from communities of the same (when available) post-fire age.

The annual legumes (Lcic) group was the richest one in the 1-yr-old communities, but its species number gradually diminished with community age. Nevertheless, representatives of this group have been recorded throughout the chronosequences, a fact indicating the successful persistence of the group. The *Aira elegantissima* group had the maximum number of species

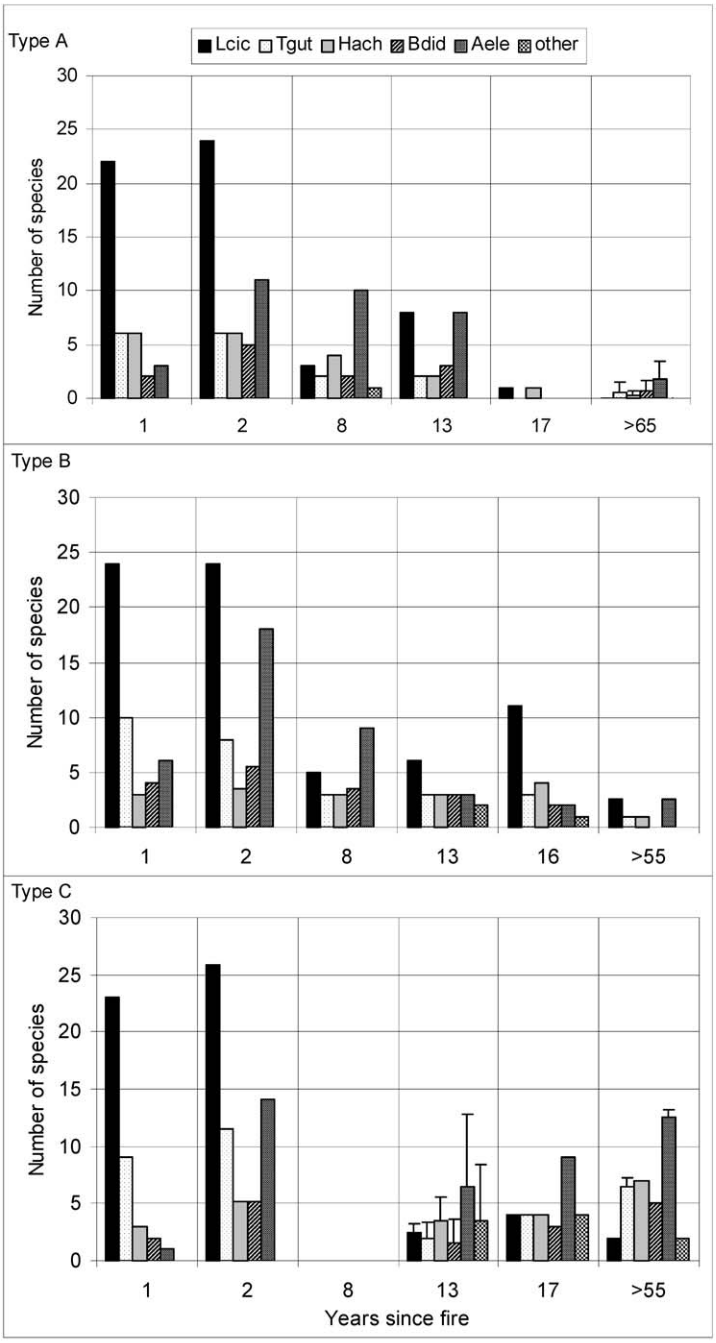

Figure 1. Species richness of annual herbaceous functional groups along communities of increasing post-fire age. Data for the most common and abundant functional groups (Lcic: *Lathyrus cicera* group, Tgut: *Tuberaria guttata* group, Hach: *Hypochoeris achyrophorus* group, Bdid: *Biscutella didyma* group, Aele: *Aira elegantissima* group) are provided separately, while for the remaining species (other) as a total. Types A, B and C refer to the various types of *P. halepensis* forests. Data for the 2^{nd} and the 8^{th} post-fire year of type B communities and for the 13^{th} post-fire year of type C communities are mean values of the two different even-aged communities. Data from all mature communities are mean values from consecutive years of sampling.

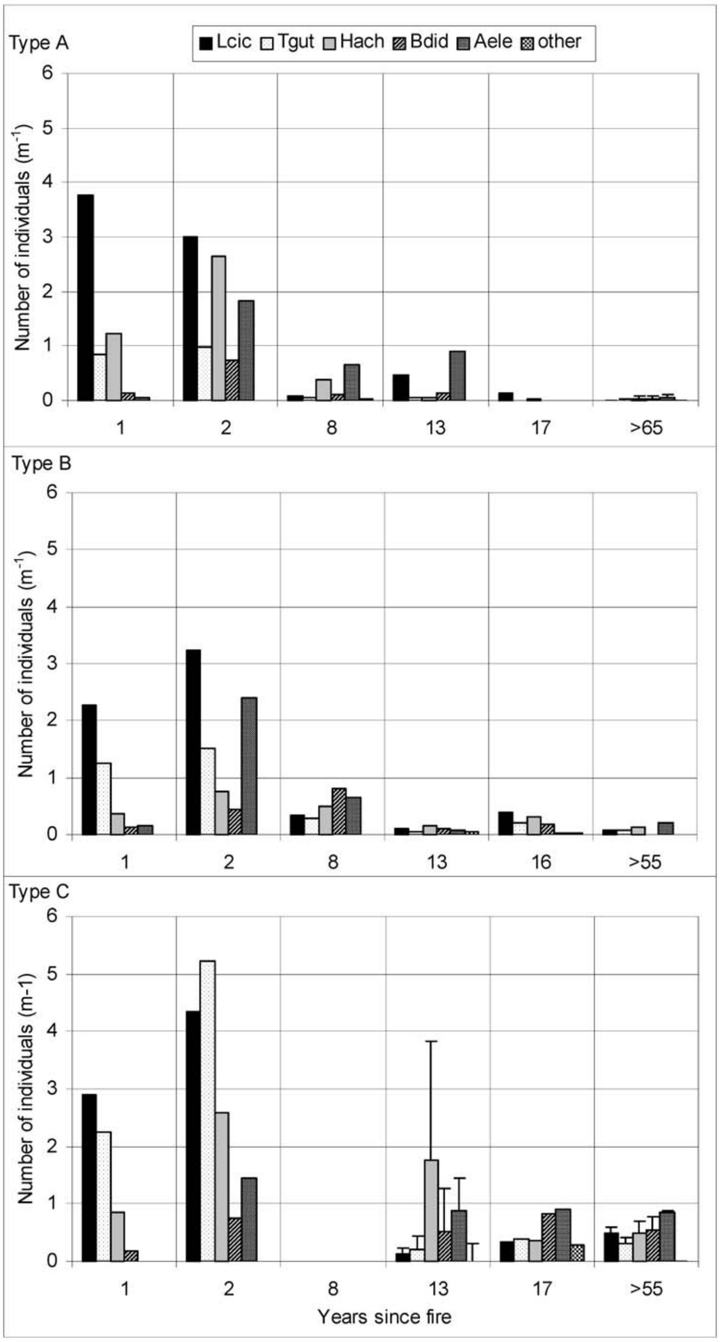

Figure 2. Species abundance of annual herbaceous functional groups along communities of increasing post-fire age. Data for the most common and abundant functional groups (Lcic: *Lathyrus cicera* group, Tgut: *Tuberaria guttata* group, Hach: *Hypochoeris achyrophorus* group, Bdid: *Biscutella didyma* group, Aele: *Aira elegantissima* group) are provided separately, while for the remaining species (other) as a total. Types A, B and C refer to the various types of *P. halepensis* forests. Data for the 2^{nd} and the 8^{th} post-fire year of type B communities and for the 13^{th} post-fire year of type C communities are mean values of the two different even-aged communities. Data from all mature communities are mean values from consecutive years of sampling.

Table 4. Number of species classified in each functional group. The total number of species recorded throughout the study is given together with the respective number from each one of the secondary chronosequences that correspond to types A, B and C of *P. halepensis* forests.

Functional Group	All communities	Type A communities	Type B communities	Type C communities
Pinus halepensis group	1	1	1	1
Crataegus monogyna group	4	3	3	-
Quercus coccifera group	11	11	10	4
Calicotome villosa group	4	3	2	2
Juniperus phoenicea group	1	-	-	1
Smilax aspera group	4	4	4	-
Asparagus acutifolius group	5	4	4	3
Erica manipuliflora group	5	2	3	4
Hypericum empetrifolium group	2	1	2	2
Genista acanthoclada group	2	2	2	2
Dorycnium hirsutum group	2	-	2	-
Cistus salvifolius group	8	7	6	7
Coridothymus capitatus group	8	6	4	5
Phagnalon graecum group	3	2	3	3
Cyclamen graecum group	31	23	21	15
Brachypodium pinnatum group	10	9	7	4
Centaurea mixta group	13	10	12	5
Convolvulus elegantissimus group	5	2	2	4
Bituminaria bituminosa group	7	4	6	4
Ajuga chamaepitys group	5	3	5	3
Stachys cretica group	5	4	3	-
Scabioza columbaria group	6	4	3	3
Cytinus hypocistis group	3	0	2	1
Lathyrus cicera group	42	31	35	25
Tuberaria guttata group	15	9	12	11
Hypochoeris achyrophorus group	9	8	7	8
Biscutella didyma group	14	11	12	7
Aira elegantissima group	48	34	42	21
Cuscuta epithymun group	2	2	1	1

in the 2-yr-old communities with a secondary peak in the mature stand of the type C communities. Some species classified as “late seeders" (Bdid goup) and annual “colonizers" (Aele group) appeared in the 1-yr-old communities with negligible densities (Figure 2), a fact that justifies our classification.

The quantitative (linear density) long-term pattern of the same annual functional groups (Figure 2) revealed the importance –at least in the early stages– of the *Tuberaria guttata* and *Hypochoeris achyrophorus* groups, which, even with a restricted number of species, they had dense populations, especially in the type C communities. Similarly to species number, the annual legumes group (Lcic) was also the group with the highest values in the 1-yr-old communities of all types.

Although the long-term change in species numbers of the functional groups that refer to woody and perennial herbaceous species was minimal, this was not the case with their change in species density. In fact, it is their pattern of abundance that determines the overall pattern of vegetation structure and physiognomy. Consequently, for both woody and perennial herbaceous species, the presented data refer to the most common and abundant functional groups. The group with the highest linear density values among perennial herbs was the group of species that show a vivid lateral growth (Bpin, Figure 3). This group retained its

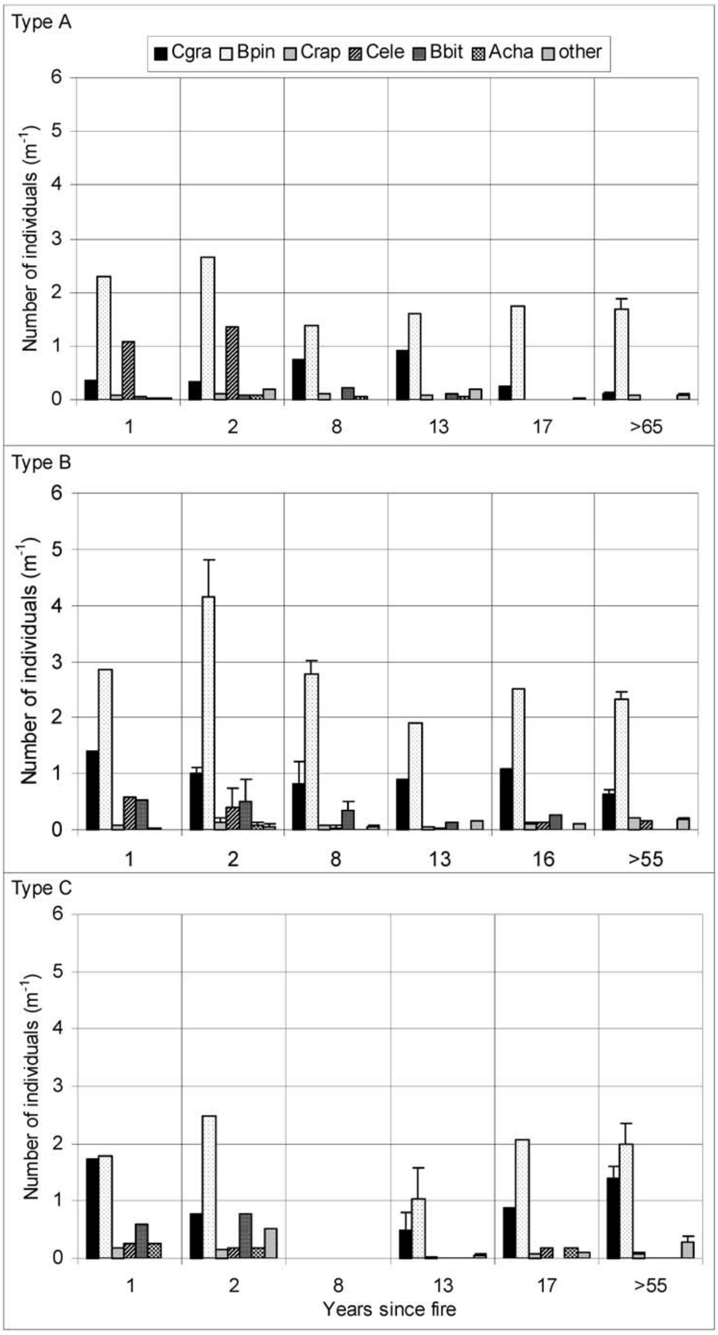

Figure 3. Species abundance of perennial herbaceous functional groups along communities of increasing post-fire age. Data for the most common and abundant functional groups (Cgra: *Cyclamen graecum* group, Bpin: *Brachypodium pinnatum* group, Crap: Centaurea raphanina, Cele: *Convolvulus elegantissimus* group, Bbit: *Bituminaria bituminosa* group, Acha: *Ajuga chameapitys* group) are provided separately, while for the remaining species (other) as a total. Types A, B and C refer to the various types of *P. halepensis* forests. Data for the 2^{nd} and the 8^{th} post-fire year of type B communities and for the 13^{th} post-fire year of type C communities are mean values of the two different even-aged communities. Data from all mature communities are mean values from consecutive years of sampling.

dominance in all sampled communities and reached its maximum in the 2-yr-old ones. The second most abundant group was the *Cyclamen graecum* group (Cgra), which had its peak right after the fire, in the 1-yr-old communities.

The long-term post-fire pattern of the various functional groups shows more striking differences among the three forest types when focusing on the woody component (Figure 4). Although the linear density of *Pinus halepensis* (the dominant species that makes a functional group by itself) is similar in the mature stands of all the three types, this is not the case when communities of younger age are compared. The maximum regeneration (in terms of established individuals) was recorded in the burned communities of Type C, while the minimum was recorded in the Type A burned communities. However, the more striking difference between A and C community types lies on the abundance of *Quercus coccifera* and *Cistus salvifolius* groups, the first being dominant in the former type of communities and the second in the latter. In the communities of Type B, *Cistus salvifolius* group was always the dominant but the *Quercus coccifera* group was not as restricted as in Type C. The high linear density values of the "other" species as far as the mature communities of types A and B are concerned, correspond to species of the woody liana group (*Smilax aspera* group), which showed their peak of abundance in the long absence of fire.

Discussion

It is widely accepted that the functional group approach is a useful tool for the evaluation of the structural and functional community complexity (Huston 1994; Diaz and Cabido 2001). To these arguments we would add that this approach is a particularly useful tool when long-term studies are involved, since the pattern of each functional group can be followed, highlighted and interrelated with the pattern of other groups.

Furthermore, the long-term functional group analysis of vegetation overcomes problems that are related to results evaluation that may occur when adopting classical approaches to vegetation analysis, namely the floristic and structural approaches (Brower et al. 1990; Burrows 1990). In the case of floristic vegetation analysis, there is always the risk of over-estimating the "ecological distance" between two communities due to "floristic distance". For example, species composition of annual herbs in the post-fire one-year-old communities of this study differed remarkably, due to initial floristic differences. When this information was "translated" to functional groups, all three communities showed similar patterns emphasizing the similar role played by fire. These kinds of problems may be more acute when communities from different geographical areas are to be compared, since floristic dissimilarity is expected to be high.

When the structural vegetation analysis is applied, the problem that might arise is of the opposite nature, i.e. the results might under-estimate the "ecological distance", when the physiognomy of vegetation is similar. For example, post-fire community development of both type B and C share a "*Cistus* dominating" phase, but different functional groups dominate in every case. In conclusion, the functional group analysis of vegetation produces results, which can be directly applicable to testing various hypotheses in an objective way.

In fire ecology studies, plants are commonly classified in groups according to their regeneration mode (Arianoutsou and Ne'eman 2000). This is useful in short-term studies but it is rather insufficient on a wider temporal scale. Other long-term post-fire studies arrange species in groups of different growth forms, life forms or plant families (Trabaud and Lepart 1980; Schiller et al 1997; Kazanis and Arianoutsou 1996; 2002). The problem of these classifications is that each group consists of species that may share some common life traits or vital attributes but not all the essential for the determination of the species long-term response towards the disturbance agent. For example, all therophytes share the fact that they are annual herbaceous plants and that regenerate by seedling establishment (Kazanis and Arianoutsou 1996), but not all of them have permanent seed banks or long distance seed dispersal ability, features that are important for understanding their long-term pattern of presence and abundance. Similarly, all legumes share the fact of forming permanent seed banks and of nitrogen fixation (Arianoutsou and Thanos 1996), but not all of them have the same growth form, life span or resprouting capacity.

In the current study, the identification of 29 different functional groups, based on species long-term post-fire response and performance, is reported. The richness of functional groups in the *Pinus halepensis* communities is higher than in the communities of mediterranean shrublands (Kazanis and Arianoutsou in preparation), a fact that emphasizes the fire

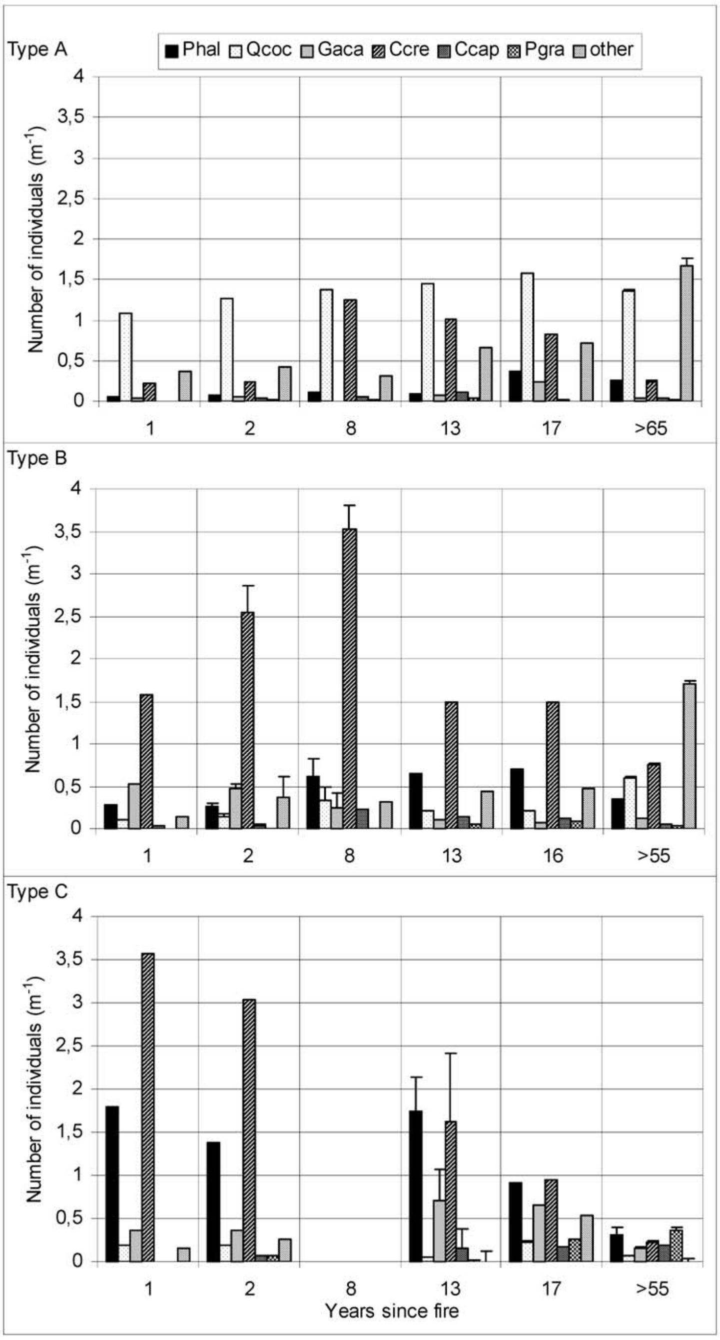

Figure 4. Species abundance of woody functional groups along communities of increasing post-fire age. Data for the most common and abundant functional groups (Phal: *Pinus halepensis* group, Qcoc: *Quercus coccifera* group, Gaca: Genista acanthoclada, Csal: *Cistus salviifolius* group, Ccap: *Coridothymus capitatus* group, Pgra: *Phagnalon graecum* group) are provided separately, while for the remaining species (other) as a total. Types A, B and C refer to the various types of *P. halepensis* forests. Data for the 2^{nd} and the 8^{th} post-fire year of type B communities and for the 13^{th} post-fire year of type C communities are mean values of the two different even-aged communities. Data from all mature communities are mean values from consecutive years of sampling.

resilience complexity occurring in the communities in question.

The contribution of several functional groups in the composition of vegetation was quite different in the three community types. The most evident differences referred to the woody component. This can be attributed to either abiotic or anthropogenic factors (Trabaud et al. 1985a; Pausas 1999a; Kutiel 2000). These changes were evident form the initial post-fire stages and may account for the observed differences in the long-term pattern of herbaceous functional groups, annuals in particular. The example of the mature stands is characteristic in this sense. In type A and B communities, where the woody component was abundant, the annual herbaceous groups were under-represented, whereas in type C communities the opposite was true.

Nevertheless, there are other functional groups that showed similar pattern of dominance in all cases. This is the case of *Lathyrus cic*era and *Brachypodium pinnatum* groups, two key-groups with different biological attributes that provide good examples of successful adaptation to the current fire regime. Species of the former group are important for compensating fire caused soil nitrogen losses with nitrogen fixation (Arianoutsou and Thanos 1996, Papavassiliou and Arianoutsou 1998). After fire, the seeds stored dormant in the soil germinate massively, making this group the richest and most abundant component of the vegetation in the first post-fire year (Papavassiliou and Arianoutsou 1993, Kazanis and Arianoutsou 1996). Persistence of this group is achieved when a small fraction of the seed bank germinates, while the vast majority of seeds remain dormant until the next fire event. In the case of *B. pinnatum* group, species are characterized by vivid lateral growth, a feature that enables them to show a better exploitation of water resources and space (Caturla et al. 2000). They resprout vigorously and massively after fire and their contribution to preventing soil erosion is of great importance. Their long life span together with their lateral growth ability ensures their successful persistence and dominance throughout the vegetation changes.

More research is needed in order to finalize the classification scheme of species that rely on seedling establishment for their regeneration. Questions on fire caused seed bank mortality, fire related germination and seed dispersal are crucial towards understanding the short- and long-term response of seeder species to fire. According to our data, there is a considerable percentage of species, most of them annuals, without any particular regeneration mode. Data from a *P. halepensis* community surveyed before and after fire support the presence of such species in such communities (Kazanis and Arianoutsou 2003). This fact does not question the applicability of the "autosuccessional" model, given the low contribution that the relative groups make to the composition and structure of vegetation (Hanes 1971; Keeley and Keeley 1981).

Ecological implications

Pausas and Lavorel (2003) have recently proposed a way of classifying species according to their response to disturbance with an approach similar to the one proposed by this study. The causal and hierarchical way of building such a functional group system may find global application in similar studies, as long as there is an adequate amount of experimental or field data about species attributes in relation to disturbance. Under the global change scenario, in particular, a lot of effort is focused on the prediction of which groups of plants will be favored or selected against by the changing fire regime (Tester 1989; Lavorel et al. 1998; Davis 1998; Pausas 1999b; Franklin et al. 2001; Arianoutsou et al. 2002). The long-term functional group approach of vegetation dynamics studies serves to this direction by permitting the production of a general model that will evaluate the fitness of different species strategies in mediterranean and other fire-prone ecosystems (Pausas 1998; 1999b; Arianoutsou 2002).

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Appendix. List of plant species classified in each functional group in the context of the current study. Within each group, families are given in alphabetical order.

FUNCTIONAL GROUP	FAMILY	SPECIES
Pinus halepensis Group	Pinaceae	*Pinus halepensis* Mill.
Crateagus monogyna Group	Fagaceae	*Quercus ilex* L.
		Quercus pubescens Willd.
	Rosaceae	*Crataegus monogyna* Jacquin
		Pyrus spinosa Forsskal
Quercus coccifera Group	Anacardiaceae	*Cottinus coggyria* Scop.
		Pistacia lentiscus L.
		Pistacia terebinthus L.
	Ericaceae	*Arbutus andrachne* L.
		Arbutus unedo L.
	Fagaceae	*Quercus coccifera* L.
	Oleaceae	*Olea europaea* L.
		Phillyrea latifolia L.
	Rhamnaceae	*Rhamnus alaternus* L.
		Rhamnus lycioides L.
	Umbelliferae	*Bupleurum fruticosum* L.
Calicotome villosa Group	Leguminosae	*Calicotome villosa* (Poiret) Link
		Colutea arborescens L.
		Hippocrepis emerus (L.) Lassen
		Spartium junceum L.
Juniperus phoenicea Group	Cupressaceae	*Juniperus phoenicea* L.
Smilax aspera Group	Caprifoliaceae	*Lonicera implexa* Aiton
	Liliaceae	*Smilax aspera* L.
	Ranunculaceae	*Clematis vitalba* L.
	Rubiaceae	*Rubia peregrina* L.
Asparagus acutifolius Group	Labiatae	*Prassium majus* L.
	Liliaceae	*Asparagus acutifolius* L.
		Ruscus aculeatus L.
	Santalaceae	*Osyris alba* L.
	Scrophulariaceae	*Euphrasia salisburgensis* Funck.
Erica manipuliflora Group	Ericaceae	*Erica arborea* L.
		Erica manipuliflora L.
	Euphorbiaceae	*Euphorbia acanthothamnos* Heldr. & Sart.
	Labiatae	*Phlomis fruticosa* L.
	Rosaceae	*Sarcopoterium spinosum* (L.) Spach
Hypericum empetrifolium Group	Compositae	*Dittrichia viscosa* (L.) Greuter
	Guttiferae	*Hypericum empetrifolium* Willd.
Genista acanthoclada Group	Leguminosae	*Anthyllis hermanniae* L.
		Genista acanthoclada DC
Dorycnium hirsutum Group	Leguminosae	*Dorycnium hirsutum* (L.) Ser.
		Ononis spinosa L.

Appendix. Continued.

FUNCTIONAL GROUP	FAMILY	SPECIES
Cistus creticus Group	Cistaceae	*Cistus creticus* L.
		Cistus monspeliensis L.
		Cistus parviflorus Lam.
		Cistus salviifolius L.
		Fumana arabica (L.) Spach
		Fumana thymifolia (L.) Webb
	Euphorbiaceae	*Euphorbia characias* L.
	Labiatae	*Satureja thymbra* L.
Coridothymus capitatus Group	Labiatae	*Ballota acetabulosa* (L.) Bentham
		Coridothymus capitatus (L.) Reichenb
		Micromeria nervosa (Desf.) Bentham
		Teucrium capitatum L.
		Teucrium divaricatum Sieber
		Thymus sp.
	Scrophulariaceae	*Antirrhinum majus* L.
	Thymelaeaceae	*Thymelaea tartonraira* (L.) All.
Phagnalon graecum Group	Compositae	*Helichrysum stoechas* (L.) Moench
		Phagnalon graecum Boiss.
	Globulariaceae	*Globularia alypum* L.
Cyclamen graecum Group	Araceae	*Arisarum vulgare* Targ.-Tozz
		Biarum tenuifolium (L.) Scott
	Aristolochiaceae	*Aristolochia microstoma* Boiss. & Spruner
	Compositae	*Scorzonera crocifolia* Sm.
	Euphorbiaceae	*Euphorbia apios* L.
	Iridaceae	*Crocus cartwrightianus* Herbert
		Crocus laevigatus Bory & Chaub.
		Crocus olivieri Gay
		Crocus sp.
		Hermodactylus tuberosus (L.) Mill.
		Iris attica Boiss
	Liliaceae	*Allium* sp.
		Allium subhirsutum L.
		Asphodeline lutea (L.) Reichb.
		Asphodelus ramosus L.
		Fritillaria graeca Boiss. & Spruner
		Gladiolus italicus Mill.
		Gagea graeca (L.) A.Terracc.
		Muscari commutatum Guss.
		Muscari comosum (L.) Mill.
		Ornithogalum sp.
		Urginea maritime (L.) Baker
	Orchidaceae	*Neotinea maculata* (Desf.) Stearn
		Ophrys lutea Cavanilles
		Orchis italica Poiret
		Orchis quadripunctata Cyr. ex Ten.
		Serapias sp.
	Primulaceae	*Cyclamen graecum* Link
	Ranunculaceae	*Anemone pavonina* Lam.
	Umbelliferae	*Bunium ferulaceum* Sm.
		Daucus carota L.

Appendix. Continued.

FUNCTIONAL GROUP	FAMILY	SPECIES
Brachypodium pinnatum Group	Compositae	*Reichardia picroides* (L.) Roth.
	Cyperaceae	*Carex* sp.
	Gramineae	*Brachypodium pinnatum* (L.) P. Beauv.
		Brachypodium retusum (Pers.) P.Beauv
		Brachypodium sylvaticum (Huds.) P.Beauv.
		Dactylis glomerata L.
		Melica ciliata L.
		Piptatherum coerulessens (Desf.) P.Beauv.
		Piptatherum miliaceum (L.) Cosson
		Poa bulbosa L.
Centaurea raphanina Group	Acanthaceae	*Acanthus spinosus* L.
	Compositae	*Centaurea raphanina* Sm.
		Crepis foetida L.
		Leontondon tuberosus L.
		Taraxacum sp.
		Tragopogon sinuatus Ave-Lall
	Gramineae	*Cynodon dactylon* (L.) Pers.
	Juncaceae	*Luzula forsteri* (Sm.) DC.
	Resedaceae	*Reseda lutea* L.
	Rosaceae	*Sanguisorba minor* Scop
	Santalaceae	*Thesium bergeri* Zucc
	Umbelliferae	*Eryngium creticum* Lam.
		Thapsia garganica L.
Convolvulus elegantissimus Group	Boraginaceae	*Alkanna tinctoria* (L.) Tausch
	Convolvulaceae	*Convolvulus arvensis* L.
		Convolvulus elegantissimus Mill.
	Malvaceae	*Malva sylvestris* L.
	Valerianaceae	*Centranthus ruber* (L.) DC
Bituminaria bituminosa Group	Leguminosae	*Anthyllis vulneraria* L.
		Astragalus monspessulanus L.
		Bituminaria bituminosa (L.) Stirton
		Onobrychis ebenoides Boiss & Spruner
		Trifolium fragiferum L.
		Trifolium physodes L.
		Trifolium uniflorum L.
Ajuga chamaepitys Group	Caryophyllaceae	*Minuartia attica* (Boiss. & Spruner) Vierh.
	Cruciferae	*Aethionema saxatile* (L.) R. Br.
		Erysimum graecum Boiss. & Spruner
	Labiatae	*Ajuga chamaepitys* (L.) Schreber
		Micromeria juliana (L.) Reichenb
Scabiosa columbaria Group	Dipsacaceae	*Scabiosa columbaria* L.
	Guttiferae	*Hypericum perforatum* L.
	Linaceae	*Linum bienne* Mill.
		Linum sp.
	Rubiaceae	*Galium aparine* L.
		Gallium melanantherum Boiss.

Appendix. Continued.

FUNCTIONAL GROUP	FAMILY	SPECIES
Stachys cretica Group	Cruciferae	*Cardaria draba* (L.) Desv.
	Euphorbiaceae	*Euphorbia myrsinites* L.
	Labiatae	*Scutellaria rupestris* Boiss & Heldr.
		Stachys cretica L.
	Scrophulariaceae	*Scrophularia heterophylla* Willd.
Cytinus hypocistis Group	Orobanchaceae	*Orobanche* sp.
		Orobanche sp.
	Raflessiaceae	*Cytinus hypocistis* (L.) L.
Lathyrus cicera Group	Leguminosae	*Coronilla scorpioides* (L.) Koch
		Hippocrepis unisiliquosa L.
		Hymenocarpos circinnatus (L.) Savi
		Lathyrus aphaca L.
		Lathyrus cicera L.
		Lathyrus saxatilis (Vent.) Vis.
		Lathyrus setifolius L.
		Lens sp.
		Lotus corniculatus L.
		Lotus ornithopodioides L.
		Medicago arabica (L.) Hudson
		Medicago disciformis DC.
		Medicago littoralis Rohde ex Loisel.
		Medicago lupulina L.
		Medicago minima (L.) Bartal
		Medicago monspeliaca (L.) Trautv.
		Medicago orbicularis (L.) Bart.
		Medicago polymorpha L.
		Melilotus sp.
		Onobrychis caput-galli (L.) Lam
		Ononis ornithopodoiodes L.
		Ononis reclinata L.
		Ornithopus sp.
		Scorpiurus muricatus L.
		Securigera securidaca (L.) Degen & Dörfl.
		Trifolium angustifolium L.
		Trifolium arvense L.
		Trifolium campestre Schreber.
		Trifolium cherleri L.
		Trifolium lappaceum L.
		Trifolium nigrescens Viv.
		Trifolium scabrum L.
		Trifolium sp.
		Trifolium stellatum L.
		Trigonella foenum-graecum L.
		Tripodion tetraphyllum (L.)Fourr.
		Vicia bythinica (L.)L.
		Vicia cretica Boiss & Heldr.
		Vicia lathyroides L.
		Vicia sativa L.
		Vicia tetrasperma (L.) Schreb.
		Vicia villosa Roth.

Appendix. Continued.

FUNCTIONAL GROUP	FAMILY	SPECIES
Tuberaria guttata Group	Caryophyllaceae	*Petrorhagia dubia* (Rofin.) G. Lopez & Romo
	Cistaceae	*Tuberaria guttata* (L.) Fourr.
	Convolvulaceae	*Convolvulus althaeoides* L.
	Cruciferae	*Eruca vesicaria* (L.) Cav.
	Euphorbiaceae	*Euphorbia taurinensis* All.
	Geraniaceae	*erodium malacoides* (L.) L'Her
		Geranium lucidum L.
		Geranium molle L.
		Geranium robertianum L.
	Papaveraceae	*Fumaria officinalis* L.
		Papaver rhoeas L.
	Primulaceae	*Anagalis arvensis* L.
	Rubiaceae	*Crucianella angustifolia* L.
	Scrophulariaceae	*Veronica cymbalaria* Bodard
	Umbelliferae	*Bupleurum semicompositum* L.
Hypochoeris achyrophorus Group	Compositae	*Atractylis cancellata* L.
		Calendula arvensis L.
		Cichorium sp.
		Hypochoeris achyrophorus L.
		Sonchus sp.
	Dipsacaceae	*Tremastelma palaestinum* (L.) Janchen
	Gramineae	*Avena sterilis* L.
		Catapodium rigidum (L.) C.A. Hubb.
		Lagurus ovatus L.
Biscutella didyma Group	Boraginaceae	*Anchusa variegata* (L.) Lehm.
		Heliotropium sp.
	Campanulaceae	*Campanula drabifolia* Sm.
	Caryophyllaceae	*Cerastium comatum* Desv.
	Cruciferae	*Biscutella didyma* L.
		Capsella bursa-pastoris (L.) Medicus
		Clypeola jonthlaspi L.
		Hymenolobus procumbens (L.) Nutt.
	Euphorbiaceae	*Euphorbia peplus* L.
	Labiatae	*Lamium amplexicaule* L.
	Linaceae	*Linum strictum* L.
		Linum trigynium L.
	Primulaceae	*Asterolinon linum-stellatum* (L.) Dudy
	Rubiaceae	*Asperula* sp.

Appendix. Continued.

FUNCTIONAL GROUP	FAMILY	SPECIES
Aira elegantissima Group	Boraginaceae	*Myosotis* sp.
	Caryophyllaceae	*Silene colorata* Poiret
		Silene conica L.
		Stellaria media (L.) Vill.
	Compositae	*Anthemis chia* L.
		Bellis annua L.
		Carduus pycnocephalus L.
		Chamomilla recutita (L.) Rauschert
		Chrysanthemum segetum L.
		Crepis hellenica Kamari
		Crupina crupinastrum (Moris) Vis
		Filago germanica Huds.
		Filago sp.
		Hypochoeris glabra L.
		Logfia gallica (L.) Coss. & Germ.
		Senecio vulgaris L.
	Dipsacaceae	*Knautia integrifolia* (L. Bertol.
	Euphorbiaceae	*Mercurialis annua* L.
	Gentianaceae	*Blackstonia perfoliata* (L.) Hudson
		Centaurium sp.
		Centaurium tenuiflorum Fritsch
	Gramineae	*Aegilops geniculata* Roth.
		Aira elegantissima Schur.
		Avena sp.
		Briza maxima L.
		Bromus madritensis L.
		Bromus hordaceous L.
		Bromus squarrosus L.
		Cynosurus echinatus L.
		Hordeum murinum L.
		Parapholis incurva (L.) CEHubbard
		Poa annua L.
		Rostraria cristata (L.) Tzwel.
		Brachypodium distachyon (L.) P.Beauv.
		Vulpia ciliata Dumort
	Papaveraceae	*Hypecoum* sp.
	Plantaginaceae	*Plantago affra* L.
	Polygonaceae	*Rumex bucephalophorus* L.
	Ranunculaceae	*Ranunculus arvensis* L.
	Scrophulariaceae	*Parentucellia latifolia* (L.) Caruel
	Umbelliferae	*Daucus involucratus* Sm.
		Lagoecia cumminoides L.
		Scandix pecten-veneris L.
		Tordylium apulum L.
		Torilis arvensis (Huds.) Link
	Urticaceae	*Parietaria* sp.
	Valerianaceae	*Valerianella dentate* (L.) Poll
		Valerianella sp.
Cuscuta epithymum Group	Convolvulaceae	*Cuscuta epithymum* (L.) L.
		Cuscuta sp.